PROCEEDINGS OF

THE LINNEAN SOCIETY OF LONDON

Session 1948–49

Vol. 161 Part 2

PROCEEDINGS OF THE GENERAL MEETING ON 10 FEBRUARY 1949

(Joint Meeting with the British Ornithologists' Union and The British Trust for Ornithology, held in the Rooms of the Geological Society of London)

Professor G. R. de Beer, F.R.S., President,
in the Chair.

With the consent of the Fellows, the ordinary business of the Meeting was postponed.

In his introductory remarks, the President expressed the Linnean Society's thanks to the Geological Society for the use of its rooms for the present Meeting.

Mr. E. M. Nicholson gave a sketch of the progress made in the recording of bird songs, with special reference to Dr. Ludwig Koch's work.

Dr. Ludwig Koch then gave his demonstration of bird-song on gramophone records. Mr. Nicholson added some comments.

Professor W. Garstang made his contribution to the Discussion, and was followed by Mr. C. Bailey, Mr. Edward A. Armstrong and Mr. James Fisher. Dr. Landsborough Thomson expressed the gratitude of the two visiting societies. The President made some concluding remarks.

[A full report of the Joint Meeting is given below.]

Before the Meeting, the President said :—

It gives me great pleasure to welcome to this Meeting members of the British Ornithologists' Union and of the British Trust for Ornithology. We are very glad to have them in our midst for our joint discussion : I cannot say, to receive them in our rooms, because you are so numerous that we have thought it necessary on this occasion to borrow the rooms of the Geological Society and I know that I am speaking for all of you when I say that it is our wish to offer our grateful thanks to the President, Council, Fellows, and Staff of the Geological Society for allowing us to meet here, and for submitting with such good grace to the trouble which we have caused them in organizing and preparing for this Meeting.

You have not come here to listen to my voice, but to hear those of the birds and I shall therefore lose no time in inviting Mr. Nicholson to open the discussion.

Mr. E. M. Nicholson, C.B., M.B.O.U., Chairman of the British Trust for Ornithology :

From the standpoint of the British Trust for Ornithology the main object of this meeting is to report progress, to demonstrate opportunities, and to appeal for co-operation in further research.

There are three partners in bird-song research, all interdependent, but not hitherto in touch. First, the ornithologist ; represented in this discussion by Professor Garstang, Mr. Armstrong, Mr. Fisher and myself. For us bird-song is an important and a baffling problem of bird behaviour—baffling chiefly because the human ear and the notebook are such fallible and inadequate tools for its scientific recording and analysis, and research has been held back for want of better tools. These tools are at last to hand.

The main new and fundamental tool has been given us by Ludwig Koch in the form of a remarkably complete and still growing library of permanent records of the actual sounds made by individual wild birds at known times and places. This is becoming for us what the British Museum collection of skins and other specimens is for the taxonomist—it is our bible and dictionary, always available to answer our questions and to put its own new questions to us.

I want here to pay tribute to the magnitude of Ludwig Koch's achievement. He came here in the troubled years not long before the war, having lost almost everything under the Nazis in Germany, and been very badly treated. Almost everything was against him. He had hardly any friends, he hardly knew the language ; he was interested in a field of research which promised great expense and difficulty for very uncertain results, and for results in which few were at that time interested. He had to spend endless hours in remote places and in even worse weather than is the normal lot of outdoor activities in England—during more than one of those breeding seasons in the mid-thirties it rained, it hailed, it blew gales, and it thundered with quite outstanding persistence while the precious weeks in which the birds still sang were running out, and recordings were ruined by a series of deafening and uncouth background noises. Then, as weather improved, re-armament and, in its train, war, filled the air almost all over Britain with such a noise of aircraft engines as had never been heard before in all these quiet places, and spoiled many hard-won opportunities. Yet, despite every obstacle, constantly short of money, working in a strange country and among that strange tribe which we call ornithologists, handicapped by ill-health and no longer young, Ludwig Koch pressed on and secured this vast collection of clear and faithful recordings, each one of which is a miracle of technical skill and ingenuity. That is an achievement which places all of us in his debt.

Ludwig Koch's success raised new problems. How was all this valuable material accumulated at his home to be preserved, processed, catalogued, and made available for research ? How was the work to be carried on when he could no longer face the great physical strain and hardships in all weathers ? The obvious solution was the creation of a Sound Institute, but this had reluctantly to be abandoned as support could not be found at the time. Then I wrote to the Chairman of the B.B.C., and, after a very sympathetic response, arrangements were completed with the Director-General, Sir William Haley, under which the Corporation would buy, process, catalogue and preserve the whole of Ludwig Koch's collection of records, and would give facilities for a scientific panel to advise on all the scientific problems involved and to develop their use as an instrument of research. That panel consists of myself, as Chairman, and of Dr. Julian Huxley, F.R.S., Dr. G. M. Vevers of the Zoological Society, Mr. Philip Brown of the Royal Society for the Protection of Birds, Mr. Peter Scott of the Severn Wildfowl Trust, and Dr. Bruce Campbell of the British Trust for Ornithology as Secretary. It is our task to form a link and a sieve between those interested in the scientific use of the Koch record collection, and the B.B.C., who are just completing the processing and cataloguing of the whole collection so that the risk of deterioration, loss, or inaccessibility for study, has been averted. It would, I am sure you will agree, be opportune on this, the first occasion when these arrangements have been publicly described, to express the indebtedness of scientists to the British Broadcasting Corporation for their timely help.

Through the work of Ludwig Koch and the British Broadcasting Corporation a large amount of new research material on bird-song is now available for science. How great and exciting the opportunities are, you will, I hope, learn before you leave this spot. But how, and how quickly, is science going to make use of them ? I hope that, as a result of this and later meetings, a few first-rate people will come forward and decide to take up the study of this bird-song material as their main research interest. I am sure that any who do so with the right outlook and the right training will discover at least as much in this field as in any other which they could take up.

I mentioned at the outset that there were three partners, all interdependent, in this new field of research. First came the ornithologists, then the recorders of bird voices, and now I must refer to the third partner—the expert on the nature of sound and on the problems of its reproduction. In the last few years, behind the great new industries of radio, television and radar, has grown up a body of knowledge and experimental techniques which is just reaching the point at which it can be married to our studies of bird-song. It offers us new tools by which we can, for instance, translate bird language from a series of fleeting sounds to a series of pictures which we can study and measure and compare visually. There is even some prospect, as you will be able to judge for yourselves this evening, that it may be possible to synthesize certain bird voices and thus analyse their basis not only by frequency but in respect of other subtler and important components. A research engineer working in this field, Mr. C. E. G. Bailey, will be giving you a brief glimpse of the contribution which the sound research specialist can make, in the course of our discussion.

My only remaining duty is to explain the reasons for choosing the particular records which Ludwig Koch will next demonstrate to you. In the first group you will find, briefly sampled, almost the entire basic vocabulary of the British crows. Crow language is almost ideal for study. It is loud, clear, of low frequency, and simple in its sound structure. Each species has developed the characteristic harsh low-pitched cry in its own way : the jay making it more rasping : the rook gruffer and more slurred ; the carrion crow and the hooded crow more resonant and rhythmic ; the raven more croaking ; the jackdaw more clipped and staccato ; and the chough more ringing ; yet the family likeness runs plainly through all. When we have analysed and compared these crow utterances we shall be much better qualified to tackle more complicated bird sounds.

The second group illustrates practically the entire known vocabulary of one rare and interesting wader, the greenshank, and compares it with utterances of the even scarcer whimbrel and of the curlew.

The third group shows another striking advantage secured for us by Ludwig Koch—a selection of spring and autumn songs of the robin, which no ornithologist before this winter was ever in a position to compare with accuracy.

Then you will hear the great regional variations in bird-song, illustrated by a series of songs of the chaffinch from different parts of Britain and the Continent ; and, finally, there will be a few fragments of birds mimicking other species. All these have been selected, not with a view to pleasing the ear—although many of them do—but to illustrate the almost endless opportunities of comparison and study which Ludwig Koch has presented to ornithologists.

Dr. Ludwig Koch gave a long series of his gramophone records of the song of birds ; and referred to the difficulties experienced in obtaining good records through the microphone. The records included the songs of the following birds :—Rook, Carrion Crow, Hooded Crow, Jay, Magpie, Jackdaw, Greenshank, Curlew, Whimbrel and Robin. The demonstration ended with a series of recordings of the song of the Chaffinch, giving its regional variations, and a series of records giving the attempts of birds to mimic one another.

Mr. C. E. G. Bailey, M.I.E.E., said that the proper analysis and classification of bird-song waited on visual representation ; he would describe the ways in which sound had been translated into visible shapes. Sounds consist of vibrations in the air : the sound of voices and instruments typically has a nearly repetitive sequence of vibrations. The time-graph of these vibrations, a sort of high-speed barograph, is one way of reproducing sound. (Fig. 1 shows the vibration-pattern of the vowel ‘ a ’ from ‘ father ’.) The mathematician Fourier showed that all repeated vibrations could be uniquely analysed into simple components, each having a frequency which is a multiple of the basic frequency of repetition (harmonically related components). This theory, very useful in the development of *reproducing* instruments (gramophone, radio) had led to a dead end in the description of *originating* instruments (animal voices, musical instruments). Trautwein and Vierling between 1925 and 1930 had indicated the way out in the tiny departures from exact repetition ; these enable the excitation of frequencies *not* harmonically related in the resonant cavities of the instrument.

Fig. 1.

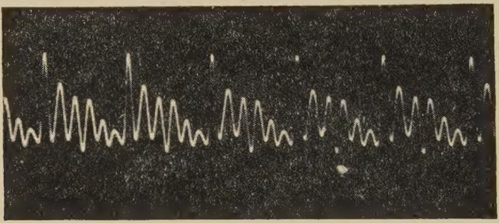
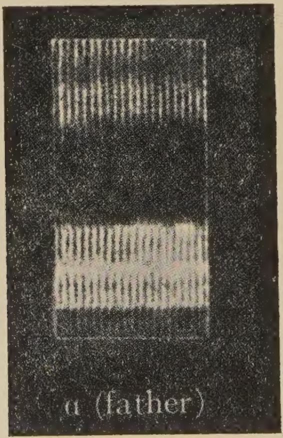


Fig. 2.



Typical animal calls can be thus analysed into a basic exciting tone and one or more non-harmonic resonance tones awakened by minute variations in

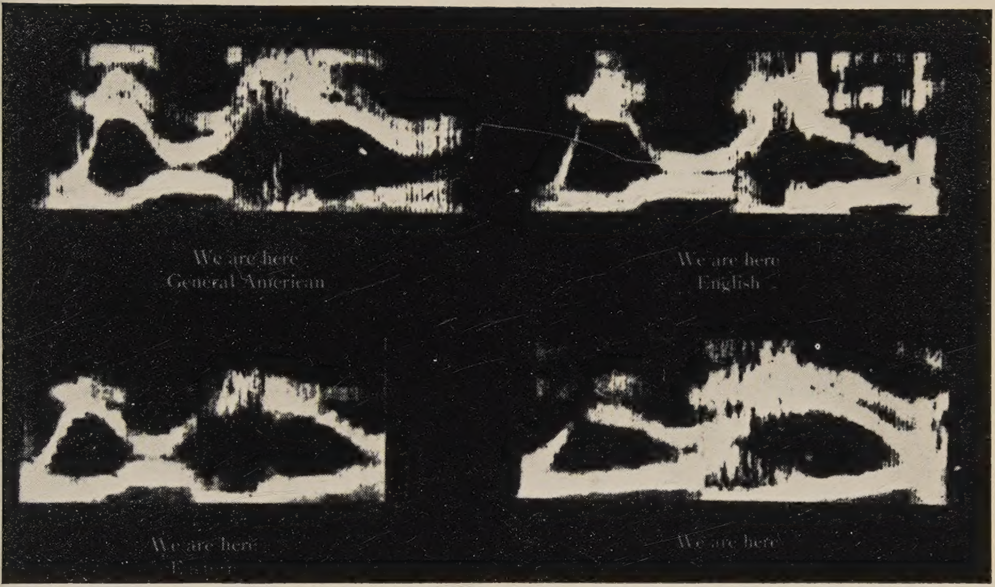


FIG. 3.

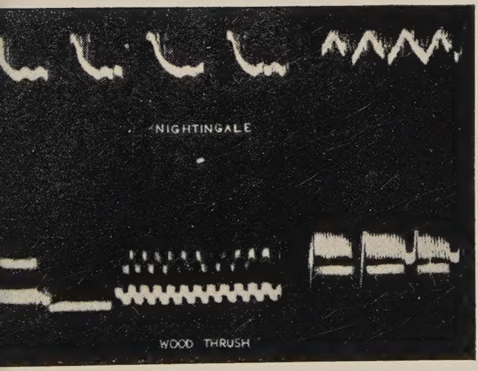


FIG. 4.

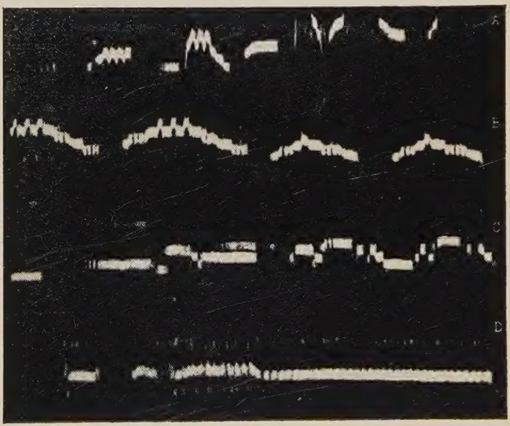


FIG. 5.

SPECTROGRAMS OF BIRD SONGS

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the basic tone. The frequency of the basic tone of birds often varies in a rapid rhythm ; below a certain speed the human ear appreciated this as a trill, above this speed as a quality of roughness (croaking).

[Mr. Bailey then manipulated the controls of an electronic apparatus to produce a basic tone, to roughen this tone, and to excite thereby a single non-harmonic resonance ; he showed by this means the synthesis of the crow's call.]

The proper instrument for studying varying unrelated frequencies is the *sound spectrograph,* in which the time-graph is drawn not of the vibrations but of the frequencies of the vibrations. This instrument has been developed in the U.S.A. by Bell Telephone Laboratories Inc. It is concise in its presentation : Fig 2 (again 'a' from 'father') covers 15 times the duration of Fig. 1. Fig. 3 (Plate **12**) shows a sentence spoken by three American voices and one English voice. It has proved possible to read spectrograms after a few weeks training. Figs. 4 and 5 (Plate **12**) show some bird songs, and indicate the possibilities for the classification by sound spectrogram.

These devices are expensive and rare ; most of them are slow to use. Mr. Bailey concluded with a plea that research students should be encouraged to analyse bird song by sound spectrograph for their theses.

(Figs. 1 to 5 are reproduced from the Journal of the Acoustical Society of America.)

Mr. Edward A. Armstrong, in his remarks, called attention to the fact that in 1909 a meeting had been held in London at which recordings of the songs of various species of American birds were heard. Until the invention of electronic methods of recording and the popularity of broadcasting had stimulated interest, progress in recording the song of birds and studying it scientifically had been small. In recent years the late Albert Brand in the United States and Dr. Ludwig Koch in this country had made great progress in this field, as the recital of records made by Dr. Koch had shown.

The study of bird song was of special importance to those interested in the psychology of birds, as song enabled us to gain insight into aspects of animal mind which are obscure and difficult to study otherwise. In regard to imitation, for example, there was little evidence amongst animals of visual responsiveness to example where non-instinctive behaviour was concerned, but vocal imitation was highly developed amongst some birds and argued a remarkable capacity for learning.

The exact analysis of bird song which was now possible by means of the study of recordings opened out the possibility that such study might be of value in systematics. Recordings made in the United States of the song of the Winter Wren, *Troglodytes troglodytes hiemalis,* showed that it differed from the song of *Troglodytes troglodytes troglodytes,* but that, none the less, the two songs showed affinities. The analysis of the frequencies of the two songs and of the relationship between the harmonics and the fundamental might throw further light on the relationship of the two species. The matter was of some interest as the evidence indicated that the wrens of Europe and Asia were descended from birds which crossed over from North America by the Bering Straits land-bridge.

Recordings showed that a bird song might include many more notes than the human ear could distinguish because of the rapidity with which the notes were uttered, quite apart from the fact that there was evidence that some of the notes uttered by birds were beyond the range of human hearing.

It was not generally realized that some birds possessed a considerable repertoire of different types of song uttered in specific circumstances. Some species, such as the wren, uttered a characteristic song when feeding the nestlings.

Mr. Armstrong congratulated Dr. Koch on his remarkable achievements in recording bird song and said that all those who had heard his delightful recital would look forward with interest to hearing the results of his further endeavours and wish him success in his work in this pioneer field.

Mr. James Fisher: The multiplicity and excellence of Dr. Ludwig Koch's gramophone records of the songs of European birds, and the possibility of the dissection, analysis and reconstruction of complex bird sounds so ably demonstrated by Mr. Bailey must convince us of the presence of a really new situation in ornithology. We should now have the basis for an assault on the outstanding problems of bird-song, and the further examination of its biological function and meaning.

Among the many things they have shown, Dr. Koch's records must have suggested to us the value of song-analysis as an auxiliary tool in taxonomic work. It will not be long now, I suspect, before accurate descriptions of bird song based on the analysis of records, or reproductions of the spectrographs described by Mr. Bailey (once ornithologists have learned to read them), will appear in the taxonomic descriptions of subspecies in print in the learned journals, or in the text-books. To a certain extent they do already, though the songs have up to now been translated into English, or rather into a notation devised to fit the human tongue. I am afraid that we have not yet developed a cadre of very good translators, though I have always admired the pioneer efforts of Professor Garstang in this field. I do not think I shall give offence if I suggest that there is a fund of innocent fun in the pages of *The Handbook of British Birds*, whose learned compilers make, or quote, many attempts to put the voices of birds into words. I commend to you the description of the song of the Jack Snipe (*Lymnocryptes minimus*), which a listener has rendered ' lok-toggi, lok-toggi, lok-toggi '.

I have always felt, and still feel, notwithstanding the techniques of Dr. Koch and Mr. Bailey, that it might yet be possible to render the song of most of the British birds into ordinary musical notation. In Africa I know that Mr. Myles North is using a pocket flute recorder to fit bird songs for transcription; he has convinced me that the difficulties of doing so are not so great as they might seem; and many of us look forward to the first publication of the results of his observations, which have been made over a period of some years.

In conclusion I would like to suggest that in twenty years' time spectrographs, or transcriptions in musical notation of the noises of animals will be regularly published in scientific papers. There will be certain difficulties in publishing gramophone discs, or metal-strip-records, as scientific documents for normal circulation, but such difficulties only exist to be overcome. Meanwhile the gramophone discs which we have heard show as what a magnificent collection of recorded sound already exists, because of the energy, drive, and (I know he will not be offended if I use the word) monomania of Dr. Ludwig Koch.

Dr. A. Landsborough Thomson said that, unlike his colleague Mr. Nicholson, he had no personal contribution to make to the discussion; but on behalf of both their societies he wished to thank the Linnean Society for having arranged this very successful joint meeting, and to express appreciation of the gracious way in which the President had conducted the proceedings.

In concluding the Meeting, the President said :—

I think that we have been privileged here this afternoon, first of all in that we have been able to enjoy the charm of the songs of birds which Dr. Ludwig Koch has with such patience and skill recorded and played to us; secondly, in that we have been informed of a new starting point in the study of the song of birds.

Nothing will ever replace the pleasures which the song of birds convey to our minds subjectively, but to this now we shall be able to add a complement, namely, the possibility of studying bird songs objectively by means of recordings as prepared by Dr. Koch with precise correlation with the ecological conditions at the time of the song, and analysed by the sonic spectrograph of which Mr. Bailey has given us so stimulating a demonstration. I look forward in particular to the results of the application of these methods to the study of local and regional variability of the song of particular species of birds such as the chaffinch, and to the comparison of the results between different regions. I think it not unlikely that we shall have to include the concept of phonoclines in our consideration of the bird population of the world. And it is already clear that no taxonomer working on birds can afford to neglect the data provided by one of the most characteristic as well as the most delightful of the activities of the animals that he studies, namely their song.

PROCEEDINGS OF THE GENERAL MEETING ON 24 February 1949

Professor G. R. de Beer, F.R.S., President,
in the Chair.

The Proceedings of the General Meetings held on 20 January and 10 February 1949, having been circulated, were taken as read and confirmed.

The following were thanked for gifts to the Library since the Meeting of 20 January 1949:—An anonymous donor, Mr. James Fisher, Mr. R. Morse, Mr. S. Gordon Smith, Dr. E. Trewavas, Mr. J. W. Walton, Professor F. E. Weiss, F.R.S., the South Australian Museum, Adelaide, and the Royal University, Uppsala.

The President reported the deaths of Professor John Percival, Dr. Edward Phelps Allis, junr., Mr. Henry Arthur Potter, Mr. Charles Daley, and Professor Walter Garstang, Fellows of the Society.

A Discussion on the Evolutionary Aspect of Colour Vision was opened by Dr. R. J. Pumphrey, who was followed by Dr. E. N. Willmer. In the general discussion the following took part:—Rear-Admiral Tufton P. H. Beamish, C.B., Professor Hamilton Hartridge, F.R.S., Dr. L. C. Thomson, Dr. H. J. A. Dartnall, Dr. M. H. Pirenne, and the President; Dr. Willmer and Dr. Pumphrey replied.

DISCUSSION ON THE EVOLUTIONARY ASPECT OF COLOUR VISION

PRELIMINARY REMARKS ON THE EVOLUTION OF COLOUR VISION

By R. J. Pumphrey.

It is fitting that a discussion of the evolution of colour vision should be opened by a zoologist rather than by a specialist in human colour vision, for a zoological training enforces an historical approach without which the study of the evolution of function is profitless. And function can no more be separated from its evolutionary history than can structure if it is to be understood. But it must be admitted, that the evidence as to the nature of colour vision in animals other than Man, is as yet scanty ; and the technical difficulties of extending it are very great. Colour vision has, however, been proved to exist in several insects especially among Aculeate Hymenoptera, Diptera and Lepidoptera and in several vertebrates, fishes, reptiles, birds and primates. It may also be an attribute of the higher Crustacea, Mollusca and Arachnida, though here proof is lacking.

The proof of the existence of colour vision in a number of animals not closely related suggests two further questions. Is the fundamental mechanism the same in all cases ? And is it utilized in a similar way ? To the first question the most definite answer obtainable at present comes from measurements of the least perceptible difference in wavelength ($\varDelta\lambda$) between pure spectral colours in different parts of the spectrum. As is well known this function has been accurately determined for man. $\varDelta\lambda$ shows three minima and two maxima in the central part of the visible spectrum and rises to very high values at the extremes. It seems significant that the position of the maxima and minima for a fish (minnow) and a bird (pigeon) coincide closely with those of man. And perhaps one may conclude (i) that at least three types of receptor with different spectral sensitivities are involved and (ii) that these three types are the same in all vertebrates. The function $\varDelta\lambda/\lambda$ for the bee resembles that for man in general form but is shifted towards the shorter wavelengths, one minimum of $\varDelta\lambda$ occurring near 3800 A. in the ultra-violet, while the insect seems to be completely blind to red. (None of these curves resembles that of a dichromat.) It may be concluded that the bee also has three or more types of photo-receptor but that their spectral sensitivities are not the same as those of the vertebrate photo-receptors. In passing it may be noted that they are probably not identical with those of Lepidoptera either; for some at least of these can see red.

It does not follow that, because these animals have a fundamentally similar (trichromatic) mechanism of colour vision, it is utilized in a similar way. There are indications to the contrary. The phenomenon of simultaneous colour contrast is known in man, but it is not obtrusive except in special circumstances and at high illuminations. Kühn, however, showed that bees trained to blue consistently visit any neutral patch of similar shape with an orange surround. If simultaneous colour contrast is as dominant a factor for bees as these experiments suggest, no object of small angular subtense will appear to them intrinsically coloured ; its apparent hue will be determined principally by the background against which it is seen.

It has also been shown that some fish and birds in the early stages of training confuse violet with red as often as with indigo and this has been taken as an indication of a closed colour circle. The effect of this is difficult to evaluate but it would appear to mean that extra-spectral purples have no separate existence as colours for such animals.

On the other hand, birds and some lizards are known to possess coloured oil droplets in a proportion of the cones of their retinae. It is well known that man unaided cannot distinguish pure spectral green from a suitable mixture of yellow and blue, but he can, of course, make the distinction if he is allowed to use filters. Since each coloured oil droplet is, in effect, a filter for its own cone, it is evidently physically possible that birds can make distinctions between impure pigmentary colours which are indistinguishable to man's unaided vision, notwithstanding the fact that the discrimination of spectral colours is the same for man and bird. From these examples it is clear that similar fundamental mechanisms may be employed to collect qualitatively and quantitatively different information about the environment.

From the fact that colour vision seems to be demonstrable in just those animals whose habits make it a very useful attribute, it might be concluded that the fundamental mechanism is present in all highly developed eyes and that it may or may not be exercised in the direction of colour vision according to need.

The demonstration by Hartline and by Granit of classes of receptors of different spectral sensitivities in the eyes of a number of animals which are almost certainly colour-blind supports this conclusion.

SOME EVOLUTIONARY ASPECTS OF MAMMALIAN COLOUR VISION

By E. N. Willmer.

(With 9 text-figures.)

Examination of the literature on the occurrence of colour vision in mammals reveals the surprising fact that it is only among the primates that there is clear and unequivocal evidence for the existence of a colour sense. It is very doubtful whether dogs, cats, horses or even bulls can distinguish colours at all. The red rag to the bull is apparently just another old wives' tale.

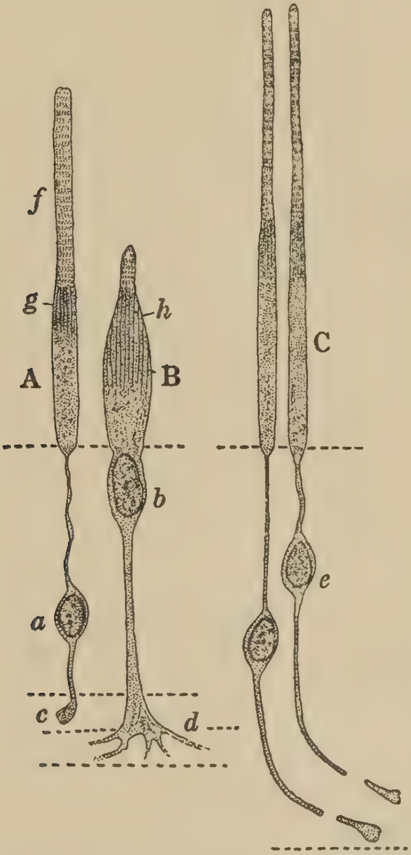


Fig. 1.—Human rods and cones (from Cajal, 1904).
A. Rod. B. Cone. C. Cones of the *fovea centralis*.

The primates probably derive from a stock of animals with nocturnal habits whose eyes were dominated by rods. Cones seem to be present in these eyes in very limited numbers, or perhaps in some cases they are even entirely absent. At this point it is perhaps desirable to be precise about the meaning to be attached to the terms rod and cone. Rods and cones (fig. 1) are two races of photo-receptor cells generally present together in the retina but in varying proportions, each race having its own peculiar properties as shown in Table I.

TABLE I.

	RODS	CONES
Outer segment	Rod-shaped	Conical
Inner segment	Cylindrical	Barrel-shaped
Nucleus	Round, very basophil	Oval, less basophil
Central connection	Fine process, terminal knob, to mop bipolar or flat bipolar	'Pedicle' to flat or midget bipolar.
Photosensitive substance	Rhodopsin	Iodopsin (?)
Maximum sensitivity	507 mμ.	570 mμ. (?)
Oil globules	Usually absent	Often present, sometimes coloured, absent in man.
Reaction to light [if any]	Myoid lengthens	Myoid contracts

Rods contain rhodopsin or visual purple and have their maximal spectral sensitivity at 507 mμ ; cones contain some other pigment or pigments (perhaps iodopsin) and have their maximum sensitivity at 570 mμ or thereabouts. The structure of the nuclei of the two groups of cells differs, the central connections are different, and there is some evidence for the existence of an antagonism between the two genera of cells ; for example, in certain fishes (e.g. *Amiurus*) and in alligators the cones contract in response to light while the rods extend. Although a typical rod and a typical cone appear very different, the structures vary considerably and the one may appear extremely like the other. Although rods possess rhodopsin there is plenty of evidence that they do not always accumulate it in the manner in which it is accumulated by the majority of the peripheral rods in man, or by the rods of the more purely nocturnal animals ; this property of accumulating visual purple or rhodopsin is better considered as a specialization for nocturnal life rather than as an inevitable property of rods. It would in fact be more reasonable to suppose that the (necessarily hypothetical) primitive cells of the rod stock possessed rhodopsin in small amounts and it was this property which made them light-sensitive in the first instance ; nature has then elaborated this property to produce the specialized rods seen in nocturnal animals and in man, and even in some of the most primitive living vertebrates. Granit (1947) has shown that ' high threshold ' rods occur in the cat and guinea-pig ; the ' green ' rod to be found in the retina of the frog is probably another example of a high threshold rod since it does not contain rhodopsin in visible amounts. Recent work (Hecht, Shlaer, Smith, Haig and Peskin, 1948) on the sensitivity of a completely colour-blind human subject has also shown that high threshold rods in all probability occur in man. It may at first sight be considered as hair-splitting to differentiate high threshold rods from cones but it is important to remember the other biological properties which distinguish rods from cones.

To return to the main argument it is clear that in the evolution of colour vision among the mammalia the main episodes relate to its evolution in the primates. In birds, by way of contrast, the mechanism for colour vision has evolved in eyes whose retinae are dominated by cones ; in the primates the mechanism has evolved from eyes largely dominated by rods. It is of course true that there is no colour vision in the primates in the absence of cones and indeed colour vision is best developed in that area of the retina where cones predominate. This however must not, without further evidence, be taken to mean that rods do not participate in colour vision. It is certainly true that there is no colour vision when rods alone are functioning, as in vision in dim light, but as will appear later, there is precisely similar evidence that there is no colour vision in man when cones alone are functioning. It seems probable that colour vision results from some differential action between rods and cones, and among rods must be included both high and low threshold rods, for there is no evidence that the low threshold rods are entirely inactive in conditions of higher illumination, though the manner in which they function may be different. The mechanism of colour vision in birds and in man may differ because of the different types of eye in which each has originated, but there is also the chance that the mechanisms may be similar and both involve interaction between rods and cones. The same applies to colour vision in fishes. In all cases rhodopsin is perhaps the key substance and it is probable that the cone pigment, as estimated from the spectral sensitivity of the cones, is, like porphyropsin in the retinae of freshwater fish, a variant of rhodopsin. The case is somewhat parallel to that of haemoglobin which is the dominant haem product in red blood corpuscles but whose place is taken by myoglobin in muscles. Rhodopsin is the dominant carotenoid-protein complex in the rods of vertebrates though in some species its place may be taken by porphyropsin, while iodopsin or some similar pigment is the form in which the complex appears when developed in cones.

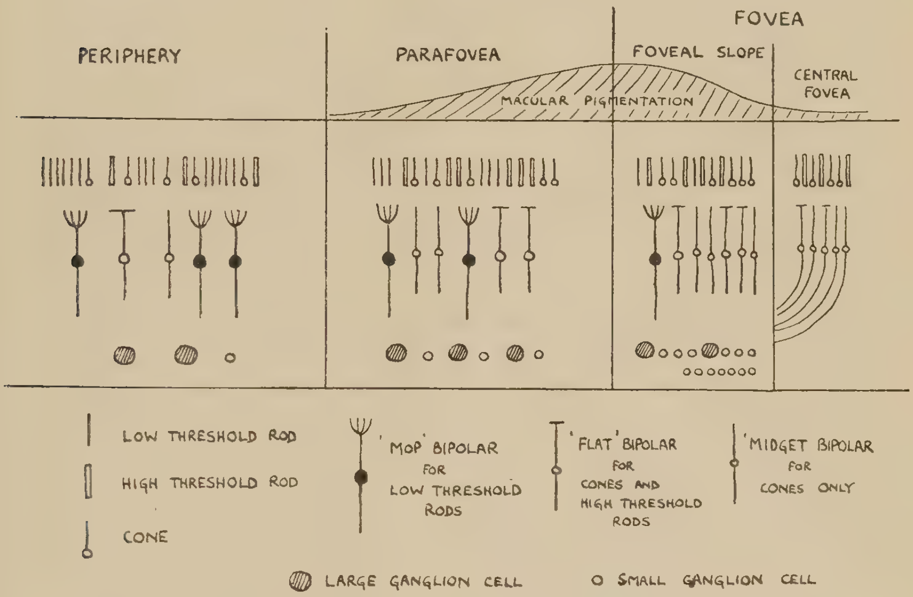


FIG. 2.—Receptors and their connections in the region of the fovea.

In the primates, colour vision is essentially connected with the fovea ; other parts of the eye of course also discriminate colours, but it is the fovea and its surroundings which achieve the highest levels of colour sensitivity and discrimination. In this area three regions should be distinguished (fig. 2). First there is the macula lutea. This is an area corresponding to a visual field of some 8 to 12° which contains a yellow pigment, chiefly among the neural and synaptic layers, and there is strong evidence that the pigment is xanthophyll (Wald, 1949). This area may be subdivided into an outer parafovea and the much smaller fovea, or pit, subtending but 2 to 3°. From this latter region the ganglion cells and bipolar cells tend to be swept away towards the periphery so that in its centre there is a flat floor, the central fovea or so-called ‘ rod-free ’ area, from which all but the receptor elements and a few of their nuclei have been removed. This floor subtends less than 1° and possesses some very distinctive properties. The region is called 'rod-free' because it does not show the property hitherto regarded as characteristic of human rods, i.e., it has very inferior powers of dark-adaptation as compared with the peripheral parts of the eye. Structurally the elements are extremely long and thin and in spite of dogmatic statements to the contrary the presence of high threshold rods must be regarded as a distinct possibility. The nuclei in the foveal centre certainly resemble those of cones, but it should be emphasized that the nuclei in this area all tend to be drawn away from the actual receptive processes and pushed away to the sides of the fovea: the nuclei left in the middle will therefore be those which started nearest the receptive processes and, by analogy with the parafovea, these are clearly the cone nuclei. The rod nuclei, being further away from the outer limiting membrane to start with, are probably drawn well away to the sides of the fovea and thus give the impression of a rod-free area in the centre. The nature of the foveal receptors is therefore uncertain, but on functional grounds it is clear that low threshold rods are very rare or absent from this area. On the other hand, the central area of the complete monochromat possesses receptors which depend on rhodopsin, but which have a high threshold and are therefore presumably high threshold rods. Their presence in the normal eye is therefore probable.

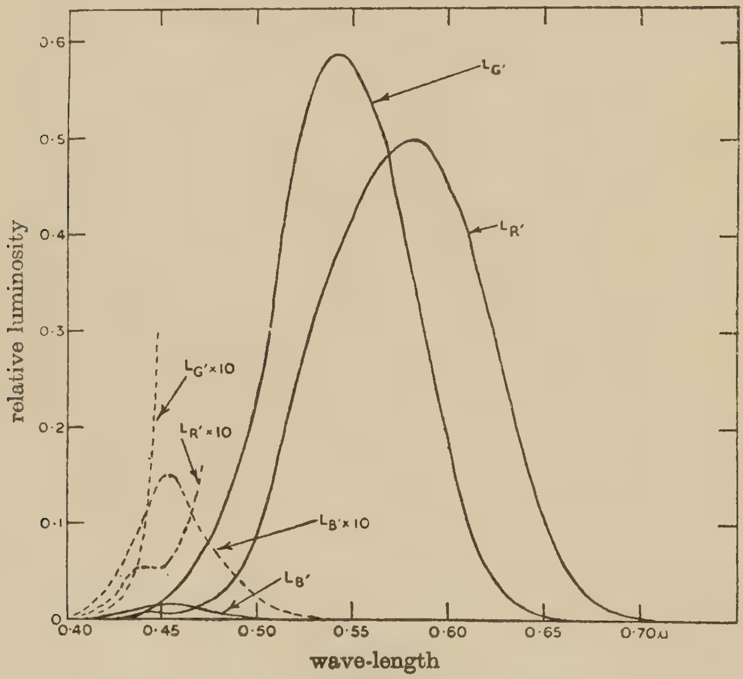
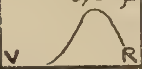
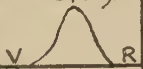
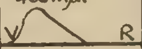


Fig. 3.—Fundamental response curves of the three colour mechanisms, red (L_R'), green (L_G') and blue (L_B'). (From Pitt, 1943.)

The fovea as a whole behaves as though it possessed three independent pathways for the perception of colour, i.e. it is triodic or trichromatic. It must have at least three types of receptor but probably does not have more, and these three must be independently connected by three separate pathways to the colour analysing centres in the brain. Colour vision is at its height in the fovea as a whole.

The central fovea, or 'rod-free' area, on the other hand, is far from perfect at colour discrimination. It behaves as a diodic or dichromatic system, and is tritanopic, i.e. it has but two pathways and makes the same colour confusions as does that rare colour-blind individual, the tritanope. If vision is confined to this area, all the spectral colours can be matched by mixtures of the spectral extremes, red and violet. If the whole eye behaves as if it had three receptors, each covering a definite region of the spectrum as shown in fig. 3, then the central fovea behaves as though the receptor which covers the blue end of the spectrum (the blue mechanism) was absent. If, as already indicated, colour depends primarily on the differences between the responses of the receptor mechanisms, then the absence of the blue mechanism does not necessarily involve the loss of blue sensation but may simply mean that blue may become indistinguishable from certain other colours. In fact, the central fovea is tritanopic but it is not blue-blind in the sense that the blue sensation cannot be aroused from stimulation of that area. Blue and violet sensations can both be aroused by stimulation of the foveal centre, but a bright violet can be matched with a blue and both can be matched with blue green if they are made sufficiently bright. It is as though the colour sensation was determined chiefly by the differences in the responses of the red and the green mechanisms but that the unique qualities of the colours were dependent upon the third or blue mechanism, again using blue, green and red merely to describe the fact that the different receptors cover these regions of the spectrum.

TABLE II.

		A "RED" 570 mμ 	B "GREEN" 540 mμ 	C BLUE 460 mμ 	NUMBER OF PATHWAYS
FOVEA	NORMAL	+	+	+	3
	PROTANOPE		+	+	2
	DEUTERANOPE TYPE I	+	+	+	2
	DEUTERANOPE TYPE II	+		+	2
CENTRAL FOVEA "ROD-FREE AREA"	NORMAL	+	+		2
	PROTANOPE		+		1
	DEUTERANOPE TYPE I	+	+		1
	DEUTERANOPE TYPE II	+			1

The colour vision properties of the normal fovea and central fovea are illustrated in Table 2, and the situation among the red-green blind is also depicted. There is every indication that the red-blind or protanope lacks the red mechanism, since his spectrum is shortened at the red end and he behaves as though he only had two independent pathways. Now, if the normal person lacks the blue mechanism in the central fovea, then the protanope may be expected to lack both the blue and the red mechanisms in this area. This would leave him with only one pathway and this should mean that he is totally colour-blind in that area and that he should be able to match any colour with any other colour. When, in fact, protanopes are made to confine their vision to the central fovea they can match any colour with any other colour and complete central fixation brings about the loss of all colour sensation. They do not see everything green (they have only the ' green ' mechanism) but, when fixation is complete and the colour sensations obtained during the process of fixation have faded, then they liken the sensation to that obtained by stimulation of the low threshold rods only, as in twilight vision. These ' sensations ', however, are fickle things upon which to base a theory and the important test in this case is that the protanope can match any colour with white or any spectral colour or colour mixture, provided that fixation is central and the brightnesses of the two matching fields are correctly adjusted.

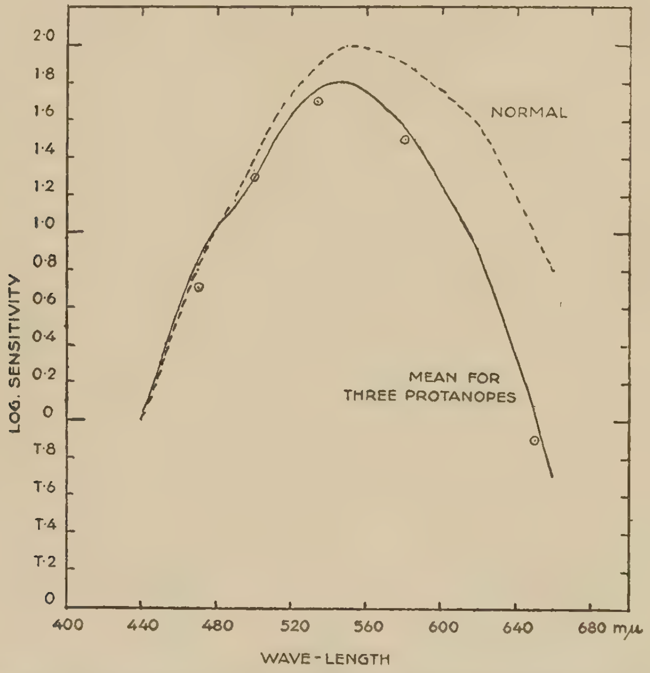


Fig 4.—Sensitivity curve for the foveal centre of protanopes compared with that of the normal observer.

The deuteranope behaves in an exactly similar way and is totally colour blind on the central fovea. Pitt (1943) has suggested that the deuteranope may have his red and green mechanisms combined. This would seem to indicate that there are three possible arrangements in the central fovea of red-green blind subjects, all of which would result in total colour blindness of this area. These possibilities are illustrated in Table 2, and there is evidence that each of the three possibilities is in fact realized.

When the spectral sensitivities of the foveal centres of complete protanopes and deuteranopes are determined it is found that these observers fall into three groups. Some, the protanopes, are relatively insensitive to the red end of the spectrum (fig. 4). Those in the second group have a spectral sensitivity which, except perhaps in total luminosity, does not differ appreciably from that of the normal person. The third group contains observers who have normal or slightly greater than normal sensitivity in the red but who become definitely less sensitive in the yellow green and throughout the whole of the rest of the spectrum (fig. 5). It is a little difficult to distinguish this effect from that which would be caused by an excess of macular pigment but the heightened sensitivity in the near red and the progressive reduction towards the green suggest some other cause, and the absence of the green mechanism is an obvious possibility. The second and third groups are both normally included in the class of deuteranopes. They match red with green on a 2° field and do not show the abnormally low red sensitivity of the protanope. On the basis of their behaviour with respect to the central fovea, deuteranopes can therefore be subdivided into Type 1 with a normal sensitivity curve, and Type 2 with a sensitivity curve which is normal or above normal in the red but falls away towards the blue end of the spectrum. These two groups may well correspond (1) to those in whom the red and green mechanisms are both present but combined into one, and (2) to those in whom the green mechanism is missing.

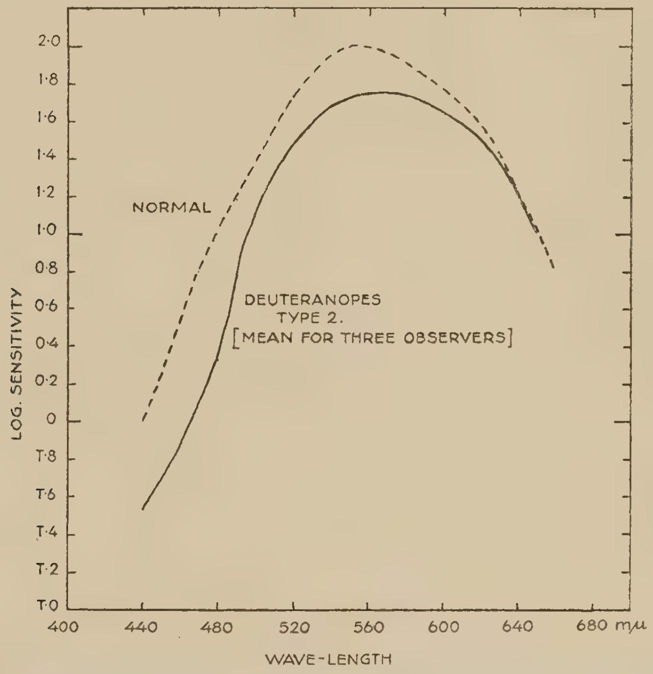


FIG. 5.—Sensitivity curve for the foveal centre of deuteranopes, Type 2, compared with that of the normal observer.

Before, however, these curves and their meaning are further discussed it will be well to adduce further evidence that single receptor mechanisms are involved. This evidence can be found by adapting the central fovea to particular wavelengths and observing the effects on the thresholds for the same and for different wavelengths. If the normal eye is adapted to either violet or red light whose brightness is around 1000 times the threshold brightness for a 20 min. field centrally fixated by the particular subject, then the sensitivity of the area is lowered for both red and violet in a characteristic manner. Violet adaptation raises the threshold to violet very extensively, but has much less effect on the sensitivity to red. Red, on the other hand, raises the threshold for red far more than it raises the threshold for violet, though, interestingly enough, the effect of equal brightnesses of red and violet on their own thresholds is less for red than it is for violet. The pattern of adaptation for the normal person is shown in Table 3, and some idea of the range of variation can also be obtained from this Table. Now, when similar adaptation experiments are performed on the deuteranopes of Type 2, i.e., those which show the trend towards insensitivity in violet end of the spectrum, the results are entirely different. In these subjects, equal brightnesses of red and violet adapting lights produce precisely similar effects on both the violet and red thresholds, indicating that there is only one receptor mechanism which is affected purely according to the brightness of the adapting light and independently of its colour.

TABLE III.

	R on R	R on V	V on R	V on V		
	(*a*)	(*b*)	(*c*)	(*d*)	*a–b*	*d–c*
NORMAL SUBJECTS.						
E.N.W.	·62	·30	·35	·90	·32	·55
H.B.	·31	·01	·18	·45	·30	·27
A.S.	·47	·35	·04	·64	·12	·60
J.N.M.	·43	$\bar{1}$·92	·16	·38	·51	·22
M.L.	·44	·15	·08	·59	·29	·51
J.W.	·59	·27	·17	·79	·32	·52
A.H.	·63	·26	·30	·71	·37	·41
MEANS	·50	·18	·18	·64	·32	·44
PROTANOPES.						
L.E.R.P.	·29	·52	·43	·59	—·23	·16
O.M.B.B.	·27	·40	·23	·34	—·13	·11
MEANS	·28	·46	·33	·46	—·18	·13
DEUTERANOPE TYPE I. [Normal luminosity curve.]						
H.V.S.	·29	0	·24	·45	·29	·21
DEUTERANOPES TYPE II. [Relatively insensitive to short wave-lengths].						
G.C.G.	·44	·39	·42	·43	·05	·01
V.H.	·31	·38	·36	·30	—·07	—·06
MEANS	·38	·39	·39	·36	—·01	—·03

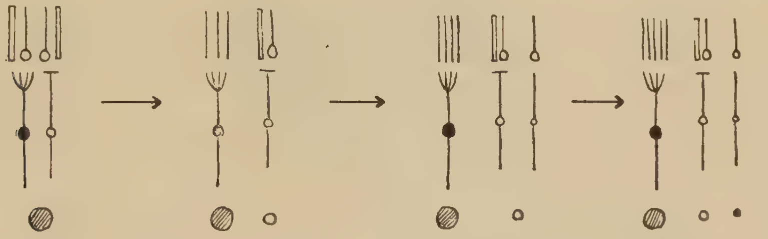
The figures represent the logarithms of the number of times the thresholds of violet or red test lights are raised by adaptation to violet or red lights of strength 1000 times threshold intensity. Central foveal fixation. R=red; V=violet.

On the other hand, a deuteranope who showed a normal sensitivity curve, when subjected to the same test with adapting lights of red and violet at 1000 times his threshold strength, showed a pattern of adaptation which fell within the normal range, as might be expected if his red and green mechanisms were both present but could not act independently.

Thirdly, when the same adaptation experiments were performed on two protanopes it was found that the red threshold was raised equally by red and violet adaptation and so was the violet threshold but the latter was raised more than the former. This observation, together with certain others on the normal observer suggest that the 'green' mechanism is not a simple one but may itself consist of more than one type of receptor connected to a single fibre. More data are, however, required on this point and for the moment it is sufficient to stress that the red threshold is equally affected by equal brightnesses of the two spectral extremes and that the same is true for the violet threshold. This, together with the fact that the protanope can match any colour with any other colour on the central fovea, clearly point to the monodic or single pathway character of the central fovea of the protanope.

Since these adaptation experiments clearly establish the single pathways of the protanope and the deuteranope Type 2, the central foveal spectral sensitivity curves of these subjects must give the spectral sensitivities of the two pathways. The deuteranope Type 2 seems not only to have but one pathway but also one receptor and so his sensitivity curve gives a measure of the spectral sensitivity of that receptor. The curve shows a maximum sensitivity in the neighbourhood of 570–580 mμ and thus, when due allowance is made for technical difficulties, remarkably near the maximum of the absorption of the only photosensitive pigment so far extracted from cones, namely iodopsin (Wald, 1937; Bliss, 1946).

The question now arises as to how these characteristics of the foveal centre can be related to the structure of that region, and how that structure has developed. The essential characteristics of rods and cones have already been outlined and it would seem reasonable to suppose that in the vertebrate ancestor, when the plan of the eye was first laid down there were both rods and cones, or at any rate cells destined to become such during the course of evolution. The rods would be sensitized by rhodopsin and the cones by a related substance, perhaps iodopsin. It is probable that such an instrument was of little more use than that of detecting the difference between light and dark and possibly determining the direction of the light, and if we may judge by the more primitive eyes in animals existing to-day the number of ganglion cells, and so of separate paths to the ‘brain’, would be small. During evolution, the vertebrate eye has proceeded to evolve three special properties (fig. 6); it has achieved an increased sensitivity by specializing some or all of its rods by enabling them to accumulate visual purple in great quantities; it has achieved an increase in visual acuity by multiplying the number of separate bipolar cells and ganglion cells relaying from the cones, with the establishment of ‘one to one’ pathways; thirdly, in special cases it has achieved the capacity for hue discrimination or colour vision. If we follow the results of the first two evolutionary processes we shall see that they in fact provide a potential mechanism for the discrimination of colour, and, not only that, but a mechanism which has most of the salient features of the colour discriminating mechanism which exists in the primates of to-day.



Primitive unspecialized eye.

Production and separation of low threshold rods as adaptation to nocturnal life.

Separation of single cones to increase acuity under daylight conditions.

Separation of complete ‘one to one’ pathway as adaption for highest visual acuity.

FIG. 6.—Scheme for the possible evolution of the pathways utilized for colour vision.

Whether this mechanism actually functions or not will, of course, depend on the parallel evolution of a cerebral or central mechanism for the analysis of the colour, and in this connection it is important to remember that colour blindness may arise, even though the retina is normal, if the necessary parallel development of the brain has failed.

The dual character of the receptor layer of the retina has already been stressed and an examination of the bipolar cell layer in the more primitive vertebrates and in the young individuals of more advanced types tends to show two categories of bipolar cells (fig. 7). These were classed by Cajal as rod and cone bipolars respectively. Polyak (1941), however, has thrown doubt on this clear distinction and is of the opinion that both types, which differ markedly in the orientation and distribution of their dendrites and end processes, actually connect with both types of receptors, the rods and the cones. The physiological nature of these connections is still unknown. Nevertheless there is more than a grain of truth in Cajal's ideas, because the mop bipolar of Polyak seems to be concerned much more with rods than cones. It connects with many rods which have no connections with any other bipolar cells and it is absent or exceedingly sparse in the region connecting with the central fovea, from which low threshold rods are also absent. Moreover, the flat bipolar is clearly the one which is more concerned with cones, and the midget bipolar, which forms the 'private' connections with individual cones, is equally clearly a derivative of the flat bipolar. The flat (and the brush) bipolars would then represent the primitive bipolar types and probably relay from both rods and cones, the rods in this case including the primitive high threshold type. It is of some significance that it is only the mop bipolar which is absent from the cells connecting with the central fovea.

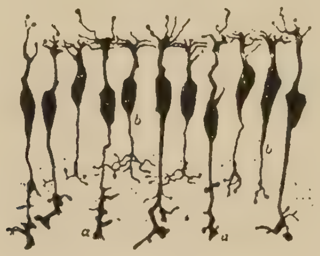


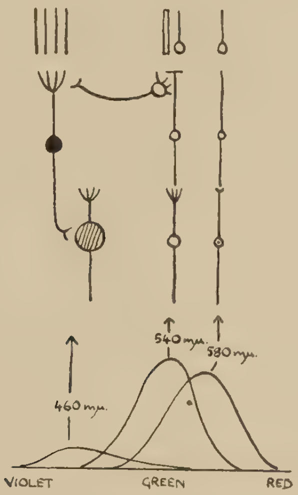
Fig. 7.—Bipolar cells from the eye of the kitten. (From Cajal, 1904.)

The two main specializations, one by the rods and mop bipolars towards vision in dim light and the other by the cones and midget bipolars towards high acuity in daylight, thus lead to the establishment of three pathways in the eye as a whole and to two in the central fovea. The three pathways are formed thus, (i) by the mop bipolar relaying from low threshold rods (which may function in an altered fashion in daylight conditions), (ii) by the flat (and brush) bipolars relaying from high threshold rods and cones, and (iii) by the midget bipolars relaying from cones only. The paths and their possible evolution are shown in fig. 6.

This evolution leads normally to a triodic eye with a diodic centre. Failure or absence of the midget bipolars would lead to a monodic centre having only the mixed rod-cone pathway. Similarly a monodic centre would result if the midget bipolars had differentiated but the necessary ganglion cells or corresponding analysing centres in the brain had failed to keep pace. Thirdly, a monodic centre would result if specialization of the midget bipolar had proceeded to completion with the elimination of the primitive mixed rod-cone pathway ;

this complete differentiation of the midget bipolar might be expected to be advantageous on the grounds of increased visual acuity and would thus have a certain survival value.

Histological structure then is consistent with three pathways for colour vision, and these are pathways which have developed for other purposes. Their use for colour vision may only have developed in those animals which have particular need for colour discrimination. If the spectral sensitivity curve of the deuteranope Type 2 represents the sensitivity of cones only, as on this hypothesis it would, then the rod-cone pathway, via the flat bipolar, would have a sensitivity intermediate between that of the high threshold rod as seen in the complete monochromat described by Hecht *et al.* (1948) and that of the deuteranope Type 2. It would have a maximum sensitivity in the neighbourhood of 540 mμ, where the maximum of the protanope is actually found and where the 'green' mechanism of the normal eye has been estimated to be most sensitive (fig. 8). The 'blue' mechanism or third pathway dependent on the activity of the low threshold rods might be expected to have its maximum at 507 mμ, but this is not the case, the maximum being between 450 and 460 mμ, as estimated from colour-mixing data. Nevertheless this does not necessarily rule out the rod-mop bipolar path as the third pathway. In the first place it would be an advantage in daylight vision that the very sensitive rods should be prevented from dominating the scene and causing dazzle. Inhibition of these rods by the cones is therefore not an unlikely result, and there is ample evidence from the work of Granit to indicate that it is the cones which seem to lead to the development of inhibitory processes in the retina. Inhibition of the low threshold rods by one or other of the units functioning in daylight would lead to a maximum sensitivity more nearly in the region of 460 mμ as required.



The 'blue' pathway could only act as such if the activity of the rods were suppressed by that of the cones. 'Horizontal' cells have dendrites on cones and their axons on rods. The synaptic connections of the 'mop' bipolar are peculiar.

FIG. 8.—Possible pathways for colour vision with their approximate spectral sensitivities.

There is now the further consideration that, to satisfy the data of colour mixing, the three pathways must be independent and that the spectral sensitivities must be different. To satisfy this condition it must be assumed that the spectral sensitivities of the high and low threshold rods in daylight conditions must be different. Two possibilities suggest themselves in answer to this requirement. First, the breakdown products of the rhodopsin in the low threshold rods may, by acting as a colour filter, alter the sensitivity of the receptor, or they may contribute by their own breakdown towards an altered sensitivity. Secondly, most of the low threshold rods are removed from the screening action of the macular pigment, while the high threshold rods of the central area are behind such a screen. Perhaps this is the reason for the existence of macular pigmentation, though here again it is more probable that it developed as an aid to the elimination of the worse effects of chromatic aberration, rather than specifically to aid colour vision.

To sum up then, it is suggested that for the purpose of colour vision the eye has made use of the three pathways which it has already developed in order to achieve greater sensitivity and higher acuity. For this reason it is likely that a similar mechanism might arise in different vertebrates widely separate in the evolutionary tree, and the sporadic occurrence of colour vision thus receives some sort of explanation ; so too do the various forms of colour blindness, for these arise as stages in the evolutionary pattern, as indicated in fig. 9, which also indicates where the protanomalous and deuteranomalous subjects fit into the scheme.

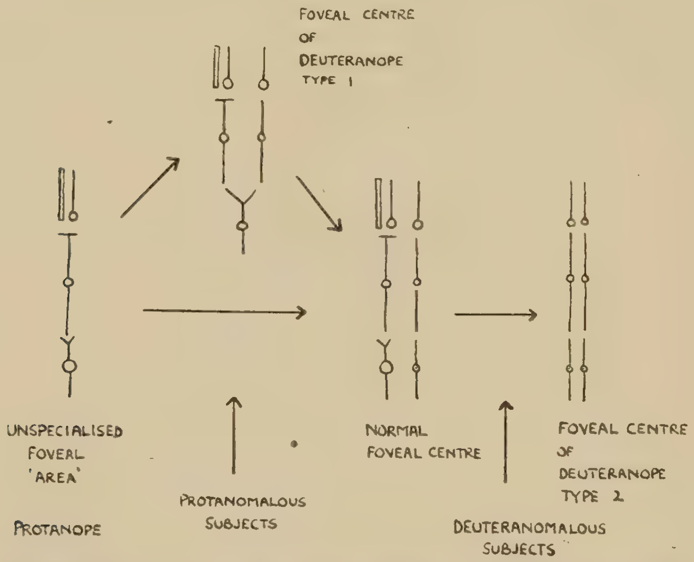

FOVEAL CENTRE OF DEUTERANOPE TYPE 1
UNSPECIALISED FOVEAL 'AREA'
PROTANOPE
PROTANOMALOUS SUBJECTS
NORMAL FOVEAL CENTRE
FOVEAL CENTRE OF DEUTERANOPE TYPE 2
DEUTERANOMALOUS SUBJECTS

FIG. 9.—Possible evolution of the foveal centre showing how the various types of colour blindness may arise as steps in the process.

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GENERAL DISCUSSION

Rear-Admiral T. P. H. BEAMISH : I fear I cannot add anything of value to the Evolutionary Aspect of Colour Vision. However, I venture to express the opinion that colour vision is of great value to human beings, and that therefore it has been and is subject to evolutionary processes.

The scientific approach and continued research is of the utmost importance, and my remarks will be confined to some practical aspects of colour vision and its defects in human beings.

Prior to 1914 or thereabouts the subject had not been scientifically explored, and the tests for colour vision were farcical. Since those days colour vision as affecting the responsible duties of sailors and airman has been placed on a scientific footing and the tests are now extremely searching and rigid.

I have always understood that some railway authorities appealed to the Admiralty to help them solve the causes of some inexplicable accidents on the railways where red and green lights were involved.

I commanded several warships between 1914 and 1918, and in one of them I had a most efficient Chief Yeoman of Signals, but I suspected his capacity for identifying flag signals and I subjected him to a simple test. Finally it became clear that he had a serious defect in his colour vision. The fault of course did not lie with him. There is another aspect of interest. At times men use any device to get out of the services, and the plea of colour blindness has been resorted to. However, a Japanese expert devised a series of coloured plates with explanatory text which was at one time available for professionals. I have a copy. The object was to frustrate malingerers, and it was completely successful. At the same time it provides an accurate but not complete means of testing the degrees of defect in colour vision. You are no doubt aware that at least 10 per cent. of men are in some degree colour blind, and that a tiny proportion of women are thus affected : and that the defect passes through the female.

I have seen a test conducted in a pitch dark room where a clear pin point of green light has been described as red by the person under test, one whose colour vision by all simple tests in daylight would never be called in question.

Prof. HAMILTON HARTRIDGE, F.R.S. : There are three points with regard to Dr. Willmer's contribution which I would like to raise ; the presence of pigments in the fovea, the presence of rods in the fovea and the absence of blue perception at the fovea.

With regard to the foveal pigments Gullstrand believed the yellow colour to be a post-mortem phenomenon. Wolff in the *Anatomy of the Eye and Orbit* (third edition, p. 103), wrote :—

'The yellow colour of the macula lutea is best seen in post-mortem eyes in which the retina has already become clouded. It is not seen in perfectly fresh eyes nor ordinarily with the ophthalmoscope.'

According to Polyak there is some pigment to be found but this is usually absent from the floor of the fovea, but is present in the sloping sides which surround that floor.

With regard to the presence of rods which Dr. Willmer has suggested in order to account for the dichromatic vision which he finds there, it is usually stated that these structures are absent, and that the centre of the fovea contains nothing but cones, the evidence being that cones elsewhere in the retina stain red when Mallory's triple stain is used. When using the same method of staining the rods appear blue. At the macula the cells present show the typical red staining of cones and no signs of blue stained elements are present. We are therefore led to the conclusion either that rods are absent or that the rods at the fovea have altered their staining characters by adopting that of the cones. Fig. 69 opposite p. 85 of Wolff's book shows a part of the macula stained with Mallory's triple stain. In this the receptors are all stained red showing that they are cones.

The writer has performed numerous experiments in an attempt to demonstrate a difference of blue perception at the fovea and in the parts of the retina which surround it, but has been unable to find any clearly marked differences. Thus a small monochromatic blue test object viewed by the fovea of one eye appears to be identical with a second similar test object viewed by the parafovea of the other eye. Moreover, Holmgren on stimulating different parts of the fovea with monochromatic blue rays distinctly saw these rays as blue in some situations. The author has confirmed Holmgren's observations.

There is no doubt whatever that on reduction of visual angle or of light intensity that a dramatic change occurs in colour vision. Thus yellow appears to be replaced by white or pale grey, while blue appears to be dark grey or black, indicating the presence of what the writer has called 'reduced foveal colour vision.' But these changes are not limited to the fovea or even to the macula, but occur, so far as can be judged, throughout the whole of the retinal area which subtends an angle of 10° or 15° with the visual axis. Thus the change of colour vision is not a matter of retinal location but of field size and light intensity.

Dr. L. C. THOMSON : Dr. Willmer's thesis on the evolutionary development of colour vision depends to a large extent upon the behaviour of colour blind subjects when investigated with a stimulus of small extent. Under these conditions protanopic subjects are said to be unable to distinguish any spectral colour from any other.

This has not been my experience when using stimulating conditions similar to those of Dr. Willmer. In a detailed study of two protanopes, one was unable to distinguish any spectral colours, but the other could distinguish them in that spectral region in which his colour vision was best with a normal size stimulus, namely at 490 mμ.

A further point. Both my two subjects were able, when first looking at the small stimulus, to distinguish colours in the spectrum around wavelength 490 mμ, the differences fading in a few seconds, and in making their settings they would enquire which criterion they should use. Thus, these two protanopes appeared to have power to distinguish certain wavelengths, which, in one case, rapidly disappeared when the stimulus was viewed steadily.

Dr. Willmer's scheme requires complete absence of colour vision in protanopes under these special conditions of observation. This my two subjects did not have, and I shall await his further experiments with great interest.

Dr. H. J. A. DARTNALL (Vision Research Unit, M.R.C.) : Dr. Willmer has suggested that the red response curve is based on iodopsin, the green response curve on a joint activity of iodopsin and visual purple, and the blue response curve on visual purple, this last response being distorted through interaction.

I understand that the iodopsin absorption spectrum is usually related to the photopic luminosity curve as a whole (cf. a recent paper by Bliss), rather than to an individual colour response curve.

Dr. M. H. PIRENNE : I should like to mention a method which would appear capable of giving quantitative information about the colour vision of animals such as insects and fishes. It is the method of the 'moving stripes', which the late Selig Hecht and his collaborators used in order to measure the visual acuity and the intensity discrimination of *Drosophila* and the honey bee. The animal responds by a reflex movement to a displacement of the pattern of stripes in its visual field. For this to take place, it is of course necessary that the animal be able to resolve visually the elements of the pattern : if the pattern appears uniform to the eye, its displacements cannot be noticed.

In this way it is possible to find out, for instance, what is the smallest difference of intensity between alternate stripes which the animal detects; that is, to measure the animal's powers of intensity discrimination.

In such an experiment, lights of different intensities but of the same spectral composition are used. Now, by varying the spectral composition as well, it should be possible to find out which spectral lights, or which mixtures of spectral lights, appear identical to the animal; and the physical intensities of the spectral lights concerned in any match of this kind could be measured. This of course would also imply knowledge of the lights which cannot be made, by any adjustment of intensity, to appear the same to the animal—lights of which we say, in the case of human vision, that they differ in 'colour'. A body of facts, the analogue of that which constitutes our objective knowledge of human colour vision, might thus, in principle, be obtained for certain animals.

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An exposition of the 'moving stripes' method will be found in

PIRENNE, M. H. *Vision and the Eye.* London, 1948.

PROCEEDINGS OF THE GENERAL MEETING ON 10 March 1949

Professor W. H. PEARSALL, F.R.S., Vice-President,
in the Chair.

The Proceedings of the General Meeting held on 24 February 1949, having been circulated, were taken as read and confirmed.

The following were thanked for gifts made to the Library since the last Meeting:—Mr. R. E. Holttum and Professor G. D. Hale Carpenter, M.B.E.

The following Fellow signed the Obligation in the Roll and Charter Book and was admitted a Fellow:—Dr. David Allardice Webb.

David Peter Maurice Guile, Eric David Hollowday and John Vaughan, B.Sc., were severally balloted for and elected ordinary Associates.

The Vice-President in the Chair reported the death of Mr. James Hornell, Fellow of the Society.

A Joint Discussion with the SYSTEMATICS ASSOCIATION, on 'Cytology as a Factor in Taxonomy' was opened by Dr. W. B. TURRILL, followed by Dr. S. MULDAL and Colonel F. C. STERN, O.B.E., M.C.

In the general discussion the following took part:—Dr. S. C. Harland, F.R.S., Prof. T. G. B. Osborn, Prof. A. D. Peacock, Dr. O. W. Richards, Dr. J. Ramsbottom, O.B.E., Dr. D. H. Valentine, Dr. E. F. Warburg, Mr. A. J. Wilmott, Dr. C. R. Metcalfe, Mr. F. C. Grigg, Mr. L. F. La Cour, and the Vice-President in the Chair; Dr. Muldal and Dr. Turrill replied.

The following papers were read in title :—

'On the Polyzoan *Cellepora pulchra* Manzoni and the Genus *Hippopleurifera*.' By ANNA B. HASTINGS, M.A., Ph.D., British Museum (Nat. Hist.). [Printed in *Journal, Zoology*, No. 281.]

'On the Polyzoan genus *Hippomenella* Canu and Bassler, and its genotype, *Lepralia mucronelliformis* Waters.' By D. A. BROWN, M.Sc., F.G.S., New Zealand Geological Survey. [Printed in *Journal, Zoology*, No. 281.]

'Edmund Davall's Note Book.' By G. R. DE BEER, M.A., D.Sc., F.R.S., P.L.S. [Printed in *Proceedings*, **161**, Part 1.]

'Three Letters from Johann Gesner to Linnaeus.' By G. R. DE BEER, M.A., D.Sc., F.R.S., P.L.S.

JOINT DISCUSSION WITH THE SYSTEMATICS ASSOCIATION, ON CYTOLOGY AS A FACTOR IN TAXONOMY

CYTOLOGY AND TAXONOMY: A TAXONOMIC STANDPOINT

By W. B. TURRILL.

In an introductory paper to a symposium an attempt should be made to outline in general terms the field to be covered. Unfortunately several biologists who are much better qualified than I am for giving such a paper asked to be excused and I have to do the best I can. No doubt faults of omission and commission will be rectified in the discussion. My standpoint must be that of a botanical taxonomist and my special references will be mostly to seed-bearing plants.

Taxonomists have, in my opinion, a twofold task : first, to provide the means of determination of organisms, and all that this includes, without which cytology or any other branch of biology speedily becomes chaotic, and, secondly, to work towards an ideal classification which shall incorporate systematically all knowledge regarding organisms. This evening's papers and discussion will, it is hoped, focus attention on how cytological research has helped and how further research can help in these two tasks.

Cytology is the study of the cell, of the structure and behaviour of all its contents. Nowadays, extra-nuclear parts of the cell are relatively neglected and there has been a concentration of research on the nucleus and particularly on the chromosomes. Nevertheless, the whole should not be mistaken for the part, cytology for karyology. The chemical and physical structure of manufactured materials, whether food, boundary walls, or waste products often gives characters of taxonomic value, as witness comparative investigations of starch grains, ethereal oils, alkaloids, etc. Protein chemistry may one day enable all plant determinations to be made and phylogeny unravelled from fragments in test tubes! Further, some cytologists and geneticists at least acknowledge inheritance of genes in the cytoplasm and plastids—plasmagenes and plastogenes. In so far as these can be recognized by their character-controlling activities they are of importance to the taxonomist. How far the development of the characters of the plastids themselves is controlled by plastogenes may not yet be known. A taxonomist must note that plastids have not been studied comparatively to the extent they should be in the Spermatophyta. They are of considerable taxonomic importance in the Algae and in the Bryophyta. It may be hoped that later speakers will refer to extra-nuclear cytology and its bearing on classification.

There are, as in other branches of biology, two aspects of chromosome study, morphology and physiology, the structure and the behaviour of chromosomes. Under the heading of morphology of the chromosomes are included their numbers, sizes, gross shapes, and even their physico-chemical constitution. Considered apart from function, chromosome morphology simply provides additional characters to the taxonomist. The taxonomic value of these characters is commensurate with their degree of stability and correlation with other characters. Both are usually high. On the other hand, unlike many other morphological and a number of physiological characters, they can only be worked out in the laboratory and are useless for extensive work in the field. The taxonomist has to keep in mind the needs of the ecologist and of the applied botanist for quick and easy determinations.

Knowledge of still greater importance to the taxonomist is gradually accruing from the study of chromosome physiology. The word ' physiology ' is here used correctly to include all activities and behaviour. It has to be accepted as a working hypothesis that genes are material particles localized in linear arrangement along the chromosomes. Whether they will later disappear into mathematical formulae is an open question. Since chromosomes and their genes have the double function of controlling the development of characters, morphological and physiological, and by their material inheritance of transmitting such control to offspring, one must expect the study of their dynamics to explain many taxonomic puzzles and thus to enable a more generally useful classification to be worked out. The full value to the taxonomist of cytology is, it must be emphasized, nothing like as great when it is merely descriptive as when it is combined with experimental genetics, and no apology need be offered if any speaker crosses the boundary from pure cytology to cytogenetics. Amongst the subjects of taxonomic importance which come under the heading of chromosome physiology first place must be given to the behaviour of chromosomes in relation to reproduction. The sequence of a normal process of fertilization followed, after intervening mitoses in the seed-bearing plants, by chromosome pairing, chiasma-formation, crossing-over, segregation, and eventually gamete formation, explains the stability of taxa. A breakdown in any part of this sequence leads to changes which may be recognized by producing sterility or by the appearance of new characters in offspring.

Botanists acknowledge the importance of cytogenetic sterility barriers in preventing or reducing crossing between taxa. They do not, with a few exceptions, even in theory, maintain that such sterility is the only cause of isolation and of specific distinction. To know the degree and the cytological causes of sterility enables the taxonomist better or more certainly to classify his species and paramorphs. In the British knapweeds, the frequent occurrence of hybrid swarms between members of the *Centaurea nigra* and *C. jacea* groups is explained by their chromosome equivalence and this combined with extensive controlled breeding shows the absurdity of describing as species the very numerous hybrids found in the wild, however distinct they may be in the sum total of their characters. On the other hand, the failure of *Centaurea scabiosa* to cross with either *C. jacea* or *C. nigra*, in the wild or in attempted artificial breeding, is undoubtedly correlated with the differences in their chromosomal sets. *C. jacea, C. nigra* and *C. nemoralis* have $2n=4x=44$, while *C. scabiosa* has $2n=2x=20$. These cytological and genetical facts confirm the taxonomist in the sectional classification now accepted for the species concerned. The accounts of the cytology of *Nasturtium* recently published by Howard and Manton led my colleague H. K. A. Shaw, to disinter older work which had been overlooked and which anticipated from the taxonomic standpoint with remarkable exactitude many of the conclusions based on the cytological findings. In *Nasturtium* the interspecific sterility barrier appears in the F_1. There are many grades and various causes of cytogenetic sterility and the taxonomist would welcome a full and up-to-date analytical account of these as one part of a study of sterility in the broadest sense. What has been called ' the flow of genes ' from one population through another, and sometimes from one taxonomic species to another, is, in part, directed by the distribution of sterility barriers and is one cause of reticulation of characters.

Failure to form functional gametes with the reduced chromosome number may be followed by that kind of apomixis in which a diploid (or polyploid) egg develops without fertilization into a viable embryo. Occasional apomixis may be commoner in the Spermatophyta than is at present realized. In some groups it is the rule. Whatever be the previous conditions establishing this behaviour, or lack of behaviour, of the chromosome system, with non-reduction and non-fertilization, the results raise peculiar taxonomic problems which can be illustrated by the dandelions. The genus *Taraxacum* occurs throughout most of the North Temperate Region and there are range outliers in the Southern Hemisphere. Handel-Mazzetti recognized 57 species in his monograph (1907). Some species have normal reduction and amphimixis. All British *Taraxaca* that have been tested have proved to be apomictic and all that have been examined cytologically have been shown to be triploid with 24 chromosomes. Thus, in dandelions and other apomicts, while sterility is by-passed and reproduction is by seeds with the advantages of fruit dispersal, pericarp protection, and a resting period, there is loss of the potentiality for gene recombination that is associated with usual chromosome behaviour. Genetically, the result is a clone that differs from a vegetative clone by seed reproduction. Rarely there can be what Darlington has called some *subsexual* behaviour with a limited amount of segregation and recombination but, in the main, there are produced numerous micro-taxa that appear to breed true. I am strongly adverse to these being called species and given binomials. Such a procedure adds to the complications of the species concept. They should be dealt with as what cytological and genetical investigations show them to be—a distinct category of apomicts. For some purposes they can be grouped into larger categories more or less equivalent to taxonomic species. How far it is worth while to distinguish the almost innumerable apomicts in *Taraxacum* may be debated.

Another result of chromosome misbehaviour is polyploidy which is taxonomically important when a multiplication of chromosome sets is followed by a return to normal fertilization and reduction but with new chromosome numbers involved. Autopolyploidy often involves marked reduction in fertility while allopolypoids are often fully fertile. Probably the majority of allopolyploids have been accepted as distinct species by taxonomists, in so far as adequate material has been examined and considered. Cytological studies, however, are bringing to light many examples of polyploidy which require careful consideration by the taxonomist. Such have been published for *Allium*, *Galium*, *Vaccinium*, *Valeriana*, *Campanula*, *Tulipa*, and other genera. It is doubtful if any one taxonomic rule should be or can be followed at present with regard to such genera. Many species have not yet been examined cytologically, and very few have been adequately examined by many examples from all parts of their distributional areas and from all their habitats, so that generalizations are premature. It can only be said that cytological data must be welcomed, studied, and given their fair value in correlation with other data in deciding the delimitation of taxa. On the other hand, they must not be over-valued or the resultant classification becomes a special not a general one.

It is to be hoped that some speakers will deal with the help cytology can give to classification of genera and families. At this level, well above that of species, it is to pure cytology that the taxonomist must look for help, since, with some exceptions, genetical experiments are impossible. The taxonomically widest hybrid I have traced in published work is that recorded by Fernald (1918) between *Cyperus dentatus* and *R*(*h*)*ynchospora capitellata*. The genera of the two parents of the sterile hybrid are placed by Pax in two different subfamilies of the Cyperaceae.

There is time only for two examples of the use of chromosome morphology at the generic level. W. C. Gregory's instructive paper on ‘ Phylogenetic and cytological studies in the Ranunculaceae ’ deserves wider notice than it has apparently received. Most, but not all,of the genera now usually accepted in the Ranunculaceae are classified chiefly on the basis of the type and number of the chromosomes. The basic numbers 5, 7, 8, 9, and 13 are recorded. The highest degree of polyploidy occurred in the 7- and 8-series with the highest 2n—numbers of 154 and 128 respectively. The chromosomal characters correlated with those of gross morphology reveal parallel development of fruit characters in different groups and thus suggest a classification which may well be more general than any yet suggested. It is significant that *Paeonia* stands isolated cytologically from the other genera of Ranunculaceae. As long ago as 1830, Bartling proposed that it should be placed in a distinct family, Paeoniaceae, and Worsdell in 1908 reached the same conclusion. Chromosome studies seem to give some support to this view.

A second example is in Berberidaceae. Langlet, Miyaji, Kumazawa, and others have considered the cytological evidence in relation to classification. In spite of some differences in the conclusions the cytologists draw from their published results, it is evident that chromosome morphology will have to be fully considered in deciding what are the affinities of the genera formerly or at present placed in the Berberidaceae. In these genera, *Nandina, Achlys, Diphylleia, Epimedium, Jeffersonia, Podophyllum, Berberis, Caulophyllum, Leontice,* and *Ranzania* the number of the chromosomes is probably of less importance than their size and shape as evidence of relationship. There is considerable reticulation of morphological characters but some of these have been insufficiently described in the monotypic genera of which suitable material is absent or scarce in this country.

An attempt must now be made to sum up these deliberately simple and general remarks. Taxonomists welcome all the help cytologists can give them. It is certain that cytological data will greatly assist in the solution of some taxonomic problems. They will, however, probably raise as many problems as they solve and for the investigation of these data must be obtained from modern developments in such other branches of biology as ecology, anatomy, and palaeontology. It might be unkind to suggest that taxonomists are less ignorant of cytology than cytologists of taxonomy but none can dispute the need for mutual education. Taxonomists would plead for cytologists to investigate material suggested by them even if it be not cytologically ideal. They would also like to see more posts filled by cytologists or cytogeneticists in institutions with botanic gardens. Many problems, such as those of reticulation of characters, require prolonged team-work of a high order of efficiency. Let us combine to solve them.

[NOTE.—Two terms are used above which it is desirable should be defined. *Taxon* (*taxa*, plural), has been employed by Prof. Lam for ‘any taxonomic group’. *Paramorph* was suggested by the late Mr. J. R. Norman for ‘any taxonomic group below the rank of species’, that is, for any infraspecific group.]

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CYTOTAXONOMY OF BRITISH EARTHWORMS

By S. Muldal.

All previous workers in the field of earthworm systematics consider the Lumbricids as a very recently developed group. It seems to have arisen from the Glossoscolicidae, and is confined, as far as endemic species are concerned, to the Palaearctic region. Exact information is lacking from Asia, but there are a few endemic species in the Himalayas, and one as far south as Calcutta. The Himalayas thus represent the line between Palaearctic and Oriental Earthworms. It is not known whether Arabia has endemic Earthworms, but Palestine, Syria and Persia belong to the Lumbricid territory. It is also uncertain whether the northern border of Africa is to be included. Japan has a single species, but the commonest species belong to *Pheretima*. The northern limit is not known in Asia.

In Europe they coincide with the limit of glaciation during the Ice Age. It is interesting that Switzerland, although covered by the ice, has 16 endemic species. Bretscher thinks that they are young species having originated where they are found now. *Lumbricus friendi*, found in South Ireland and elsewhere only in the Pyrenees and the Alps, was considered by Southern to be a similar case.

The Lumbricids show an exceptional capacity for spreading and have almost completely conquered the Palaearctic region for themselves. The only other group which enters is Hormogastrinae, a subfamily of Glossoscolicidae, which is represented in Sardinia, Corsica, Italy, Sicily, Tunis and Algeria.

In the Nearctic division the northern limit is not known, but Canada has no endemic Earthworms. On the south, Mexico and Lower California are excluded. In this territory there are found some endemic species in the east, but most Earthworms in N. America are the same species as in Europe, and are introduced. (Stephenson : Oligochaeta.)

The systematic division of Lumbricidae is one of the difficult problems in the Oligochaeta. Michaelson, who seems to be the only worker with intimate knowledge of all the different Oligochaeta, divided Lumbricidae ('10) in :

Genus *Lumbricus.*

Genus *Octolasium.*

Subfamily Helodrilus.

Helodrilus was split up into : *Allolobophora, Eisenia, Eiseniella, Bimastus, Dendrobaena* and *Helodrilus* (now : *Eophila*). Later workers disposed of the subfamily, and regarded the components as good genera.

But there are a lot of difficulties in using this system :

1. Allolobophora—Dendrobaena : There are species of *Dendrobaena* with D-arrangement of seminal vesicles (in segm. 9–11, 12), but with closely paired setae (A-character).
2. Allolobophora—Octolasium : Species of *Octolasium* with poorly developed testes sacs, described by Michaelson as regression.
3. Eophila—Bimastus : A sharp division impossible. Ex : *E. norwegicus* with spermathecae, but closely related to *Bimastus* in other characters. *E. taschkentensis* has no spermathecae.
4. Bimastus—Dendrobaena : *B. constrictus* like *D. rubida.*

5. Eisenia—Bimastus : *Bimastus* has as generic character two pairs of seminal vesicles. Michaelson in ‘ Das Tierreich ’ states that *Eisenia* has 3 to 4 pairs of seminal vesicles. There are, however, *Eisenia* spp. with two seminal vesicles, and the number of seminal vesicles is evidently of no importance as a generic character of *Eisenia.*
6. Eisenia—Dendrobaena : *Eisenia* has spermathecal pores near the dorsal line, with an unpigmented glandular modification of the integument near the pores. *D. attemsi* has this E-mark. There is also variation in the position of the pores in *Eisenia* spp., many of which have pores in same place as *Dendrobaena* spp. Michaelson : Either *Dendrobaena* gives rise to *Eisenia* or vice versa.
7. Eisenia—Eiseniella : The number of segments occupied by the gizzard is the only valid distinction between the two genera, but even this character seems questionable : *Eiseniella* has a gizzard confined to two segments, in *Eisenia* three intermediates occur.

Chromosome numbers in the different genera of Lumbricidae.

It is possible that the chromosome number and morphology may give a new clue to the affinities of the species of Earthworms. My work on the cytology of the reproductive systems of these animals, has revealed some chromosome numbers in British species :

LUMBRICUS		
x–18	*L. terrestris*	2n–36
	L. castaneus	2n–36
	L. rubellus	2n–36
	L. festivus	2n–36
ALLOLOBOPHORA	*terrestris* f. *longa*	2n–36
x–18	*nocturna*	2n–36
	caliginosa	2n–36
x–16	*chlorotica*	2n–32
	icterica	2n–32
OCTOLASIUM	*cyaneum*	2n–180
x–18		
EISENIA		
x–18	*E. venata typica*	2n–36
	E. venata hibernica	2n–36
x–11	*E. foetida*	2n–22
x–27	*E. rosea*	2n–54
EISENIELLA		
x–18	*E. tetraedra typica*	2n–72
	E. tetraedra hercynia	2n–72
DENDROBAENA		
x–17	*D. mammalis*	2n–34
	D. rubida	2n–34
	D. subrubicunda	2n–68
BIMASTUS	*Eiseni*	2n–32
x–16		

Suggested affinities :

LUMBRICUS and OCTOLASIUM :

All species of *Lumbricus* examined had the same chromosome number, 2n–36, this may be considered as a primitive number in the family. *Octolasium cyaneum*, the only species of this genus examined, had 2n– ca 180, is assumed to be a decaploid, with basic number 18, derived from *Lumbricus* or a common ancestor.

ALLOLOBOPHORA :

The numbers here are 36 or 32. Of British species at least, the 32-group differs from the others in having more than two spermathecae, and the active part of the clitellum (the part occupied by the puberty tubercles), covers five segments. By the loss of one pair of chromosomes from the main number 36, the ancestor to *Dendrobaena* (34) might have arisen. *Dendrobaena subrubicunda* is an allotetraploid.

DENDROBAENA.

From the further loss of one pair, one would get to the other.

ALLOLOBOPHORA.
BIMASTUS.

Allolobophora number, 32, a number which is also found in *Bimastus*.

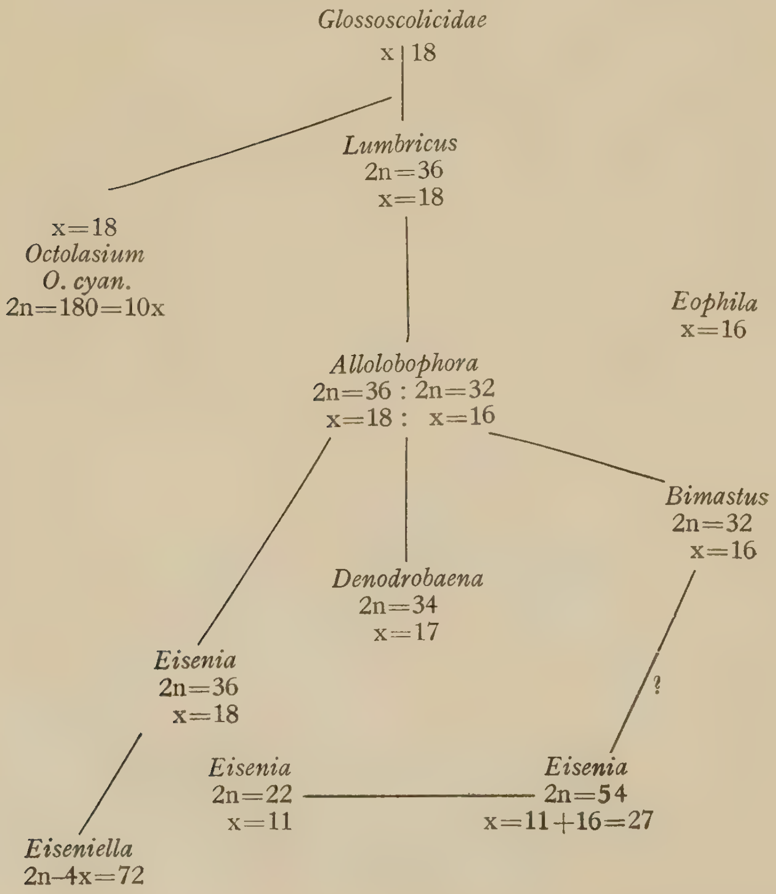
EISENIA :

The chromosome numbers in this genus are 2n–22, 36 and 54. 36 is found in *Eisenia venata*, probably derived from the 36-group of *Allolobophora*. The similarity in distribution of the different varieties of *E. venata* and those of the tetraploid (2n–72) *Eiseniella tetraedra*, suggests close relation.

EISENIELLA.

EISENIA.

Eisenia foetida has the lowest Lumbricid number, 2n–22, and *E. rosea* has 2n–54, x–27. From the presence here of some large chromosomes found also in *E. foetida*, it is suggested that the number 54, has resulted from a cross between 16 and 11, whereupon the complement was doubled—a process well known in hybrids.



CHROMOSOME NUMBERS AND TAXONOMY

By Colonel F. C. Stern, O.B.E., M.C.

(With folding map and five text-figures)

Darlington (1940) says ‘Chromosome studies unrelated to the evidence of experimental breeding have another bearing on systematics, namely in the elucidation of relationships between species and larger groups that will not cross’.

I will try and show how chromosome numbers in flowering plants form an additional basis of taxonomy which confirms external differences between species where these differences are close or difficult to distinguish, and secondly, how chromosome numbers and/or the shapes of chromosomes at mitosis may indicate the evolution or phylogeny of a species in a genus or of a genus in a family and may therefore be an aid to their classification.

The chromosome numbers in different genera can be divided into two categories—those genera where all the species have the same basic number like *Rosa* and those genera where the species have different basic numbers like *Crocus*. In some of the latter type of genera it will be found that a genus contains several different basic numbers but in some of the sections or subsections of that genus the species may have the same basic numbers like *Primula*.

Again, the genera whose species have the same basic number can be divided into three categories :

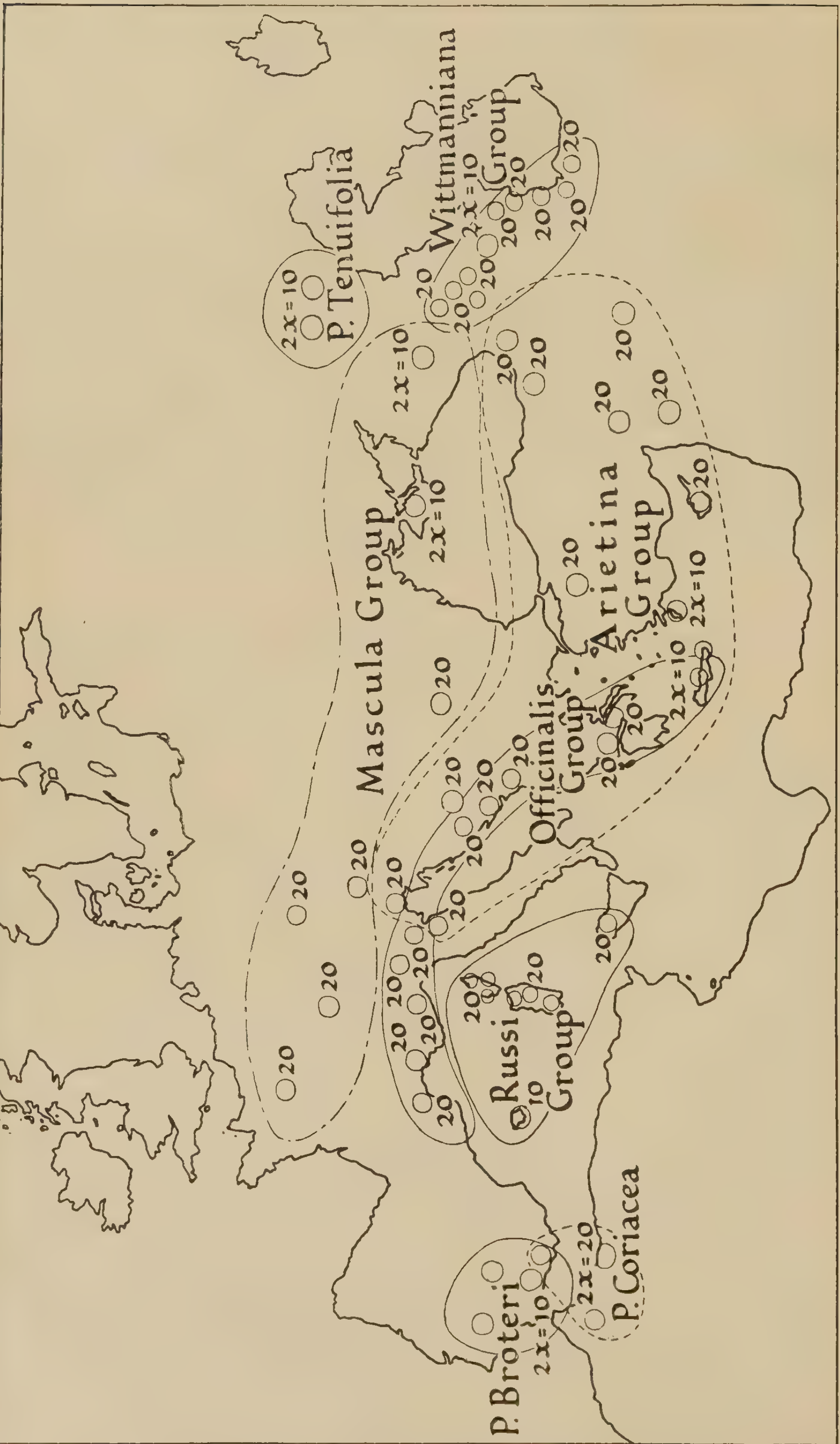
(1) where all the species are diploids or triploids as in *Lilium* ;
(2) where some species are diploids and others tetraploids as in *Paeonia* ;
(3) where there are diploids, tetraploids and greater polyploids as in the sub-section of the Farinosae section of *Primula*.

In the genera where the chromosome numbers differ it may be possible by looking at a map of the distribution of the species to see how phylogeny of the genus could have arisen.

The first map will illustrate the distribution of *Paeonia* wherein there are only diploid and tetraploid species. This genus is distributed in the Northern Hemisphere. In N. America the species are diploids, in Asia all the species except one are diploids, but in Europe including Asia Minor and the Caucasus there are 7 diploid species and 14 tetraploid species. In a paper before this Society in 1944 I have shown how I suggest the evolution of this genus has occurred ; how the diploids are confined to the southern part of Spain and the Islands of the Mediterranean and the area of the Caucasus, and how the tetraploids in each case with a larger distribution have emigrated (northwards or westward) as the Continent got warmer after the Glacial Period.

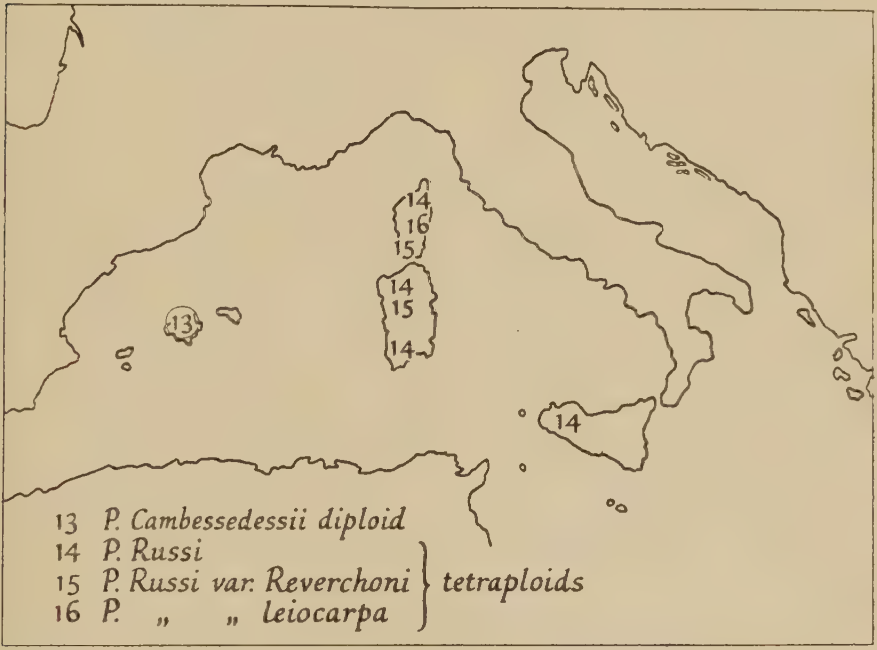
There are two examples in *Paeonia* where the chromosome number is a valuable taxonomic character :

(1) In the Russi Group of *Paeonia* the specimens in herbaria of *P. Cambessedesii* indigenous to the Balearic Islands, and *P. Russi* var *leiocarpa* only found in Corsica, are much alike but, when growing, can be distinguished by small differences not easy to describe. The differences were confirmed when it was found that *P. Cambessedesii* is a diploid and *P. Russi* var. *leiocarpa* is a tetraploid.
(2) The same thing applies to the yellow flowered paeonies of the Caucasus where the morphological differences between the two species are not great. It was found that *P. Mlokosewitschi* indigenous to a small area is a diploid and *P. Wittmaniana* with a larger distribution is a tetraploid.



MAP 1.—Map of Europe showing distribution of species of *Paeonia* with the diploid species marked 10 and the tetraploid species marked 20.

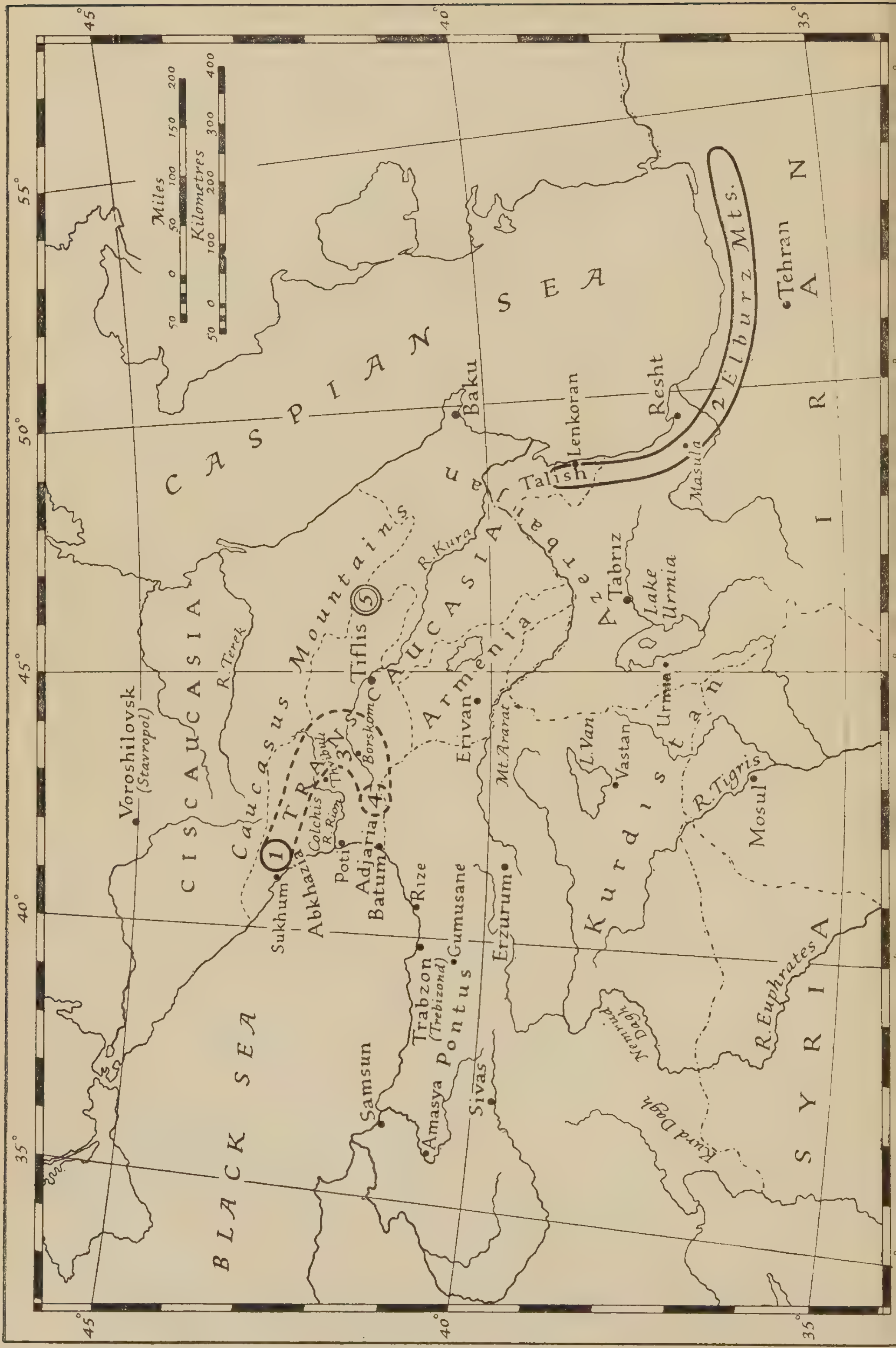
The next map illustrates the distribution of the species of the sub-section Eu-Farinosae of the Section Farinosae of the Genus *Primula*, according to Wright Smith and Fletcher (1943). In this sub-section there are diploids, tetraploids, and greater polyploids. The basic number of all species of this sub-section outside Tibet and western China is 9. Diploids are found in the northern Balkans and the Caucasus, central Asia and Japan. The distribution of one of these diploids, *P. farinosa*, is widespread through Europe, with the exception of Greece and Ireland, throughout central Asia to the Altai and Tien Shan. The other species of this sub-section are mostly more restricted in their range. In eastern central Europe the tetraploid *P. longiflora* appears, while the hexaploid *P. scotica* is indigenous to northern Scotland. Octoploids appear under the more severe climatic conditions in northern Scandinavia with *P. scandinavica*; in Labrador and Nova Scotia with *P. laurentiana*; in the Falkland Isles, Cape Horn and the southern Andes with *P. decipiens* and in the alpine area of southern Persia with *P. capitellata*. Then a species, *P. stricta*, with 126 chromosomes, 14 times the basic number of 9 (possibly the unreduced progeny of *P. scotica* (54) and *P. scandinavica* (72)) appears throughout the Arctic and sub-Arctic in Europe, Asia and N. America.



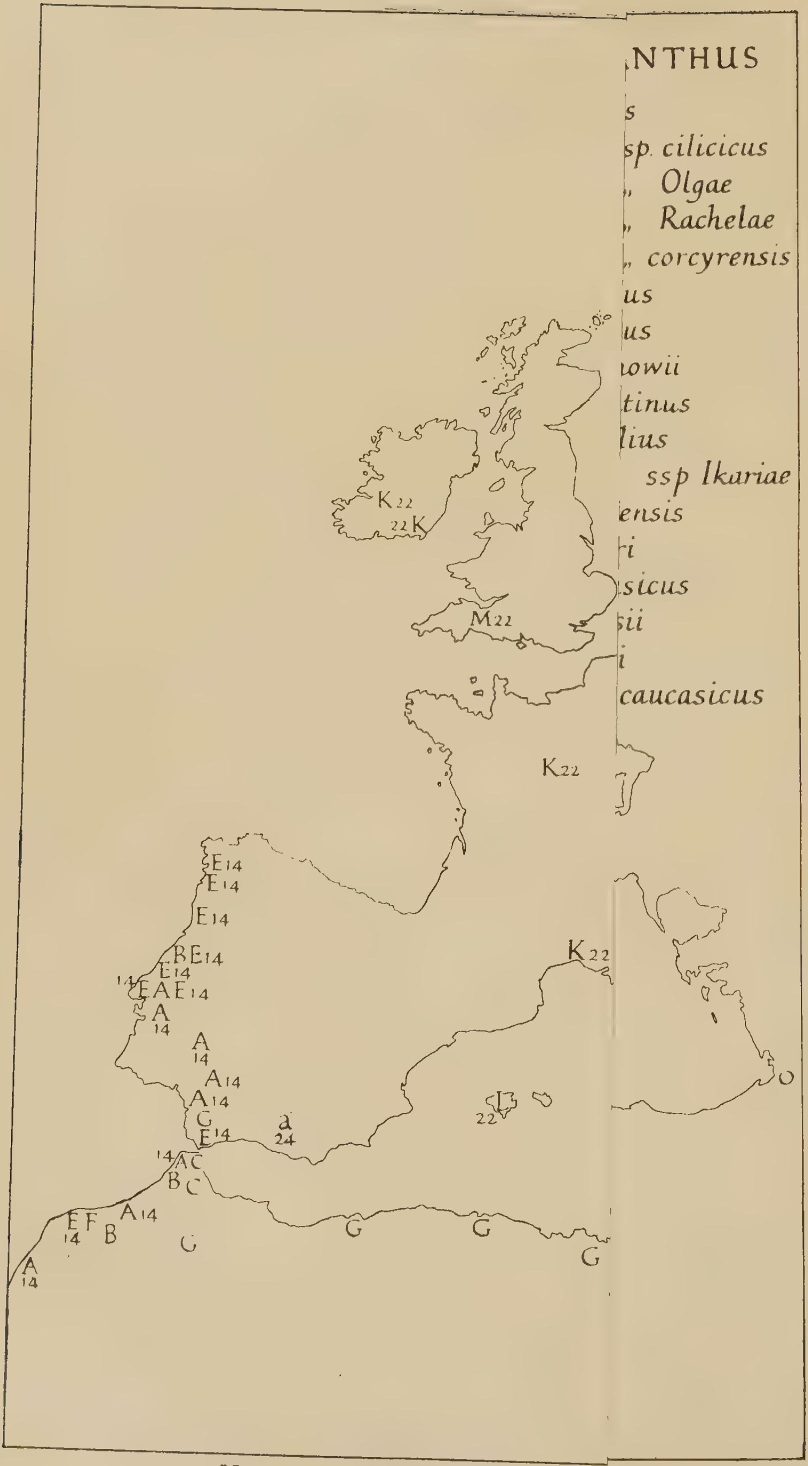
MAP 2.—Map of Europe showing the distribution of the Russi group of *Paeonia*.

Here again are instances of the value of the chromosome number, firstly in definitely separating *P. scotica* and *P. scandinavica* which morphologically are difficult to distinguish, and secondly in the phylogeny of this sub-section showing how possibly *P. farinosa* came from central Asia through the Caucasus to the Balkans and then by polyploidy invading the North and West, and possibly during the Glacial Period descending the Andes where it has remained in the more temperate area of the South.

Dr. Janaki Ammal has worked out the chromosome numbers of two other genera, *Magnolia* and *Morus*, the Mulberries, wherein there are diploids, tetraploids and greater polyploids. She has shown how the evolution of these genera may have occurred. The work on *Magnolia* has not yet been published but her work on *Morus* was in the *R.H.S. Journal*, vol. lxxiii of April 1948.



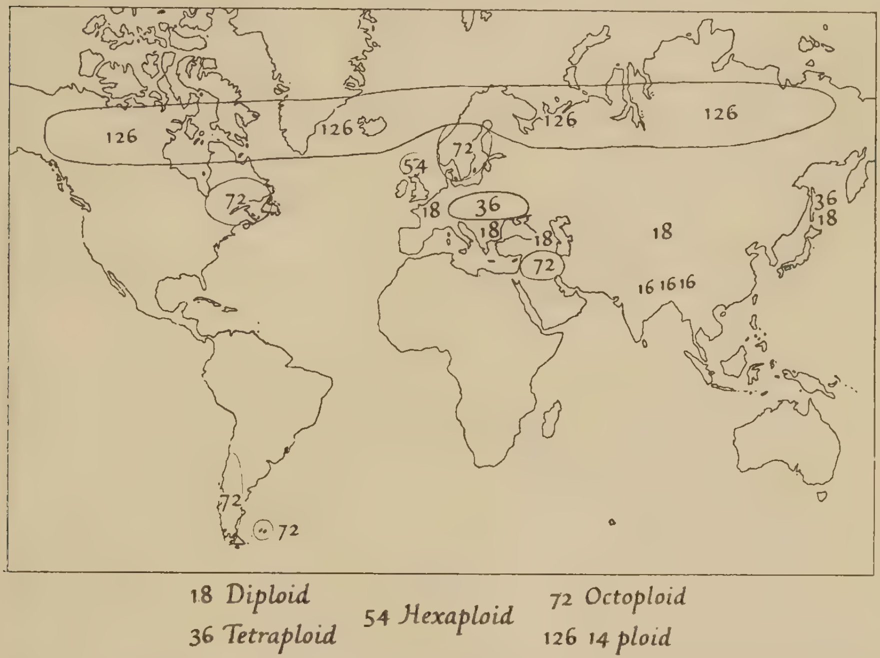
MAP 3.—Map of the Caucasus and adjacent regions showing distribution of the Wittmanniana group of *Paeonia* :—1–4. *P. Wittmanniana*, sensu lato ; 1 and 2. *P. Wittmanniana* sensu stricto sec. F. C. Stern ; *P. Wittmanniana* var. *nudicarpa* ; *P. Wittmanniana* var. *macrophylla* ; 5. *P. Mlokosewitschi*. The general ranges are based mostly on data from Busch, 1901–03.



MAP 5.—Map of Europe showing the

[*To face p.* 123.

Morus is a particularly interesting genus as the basic number of the genus is 14 and one species, *Morus nigra*, the Black Mulberry, has the chromosome number of 308, the highest number yet recorded in seed-bearing plants.



MAP 4.—Map illustrating the distribution of the species of the sub-section Eu-Farinosae of the section Farinosae of the genus *Primula*, showing the chromosome numbers of each species.

The next map shows the distribution of the genera *Leucojum* and *Galanthus*. *Leucojum* is an example of a genus containing species with different basic chromosome numbers, and *Galanthus* a genus containing species with the same basic number.

The basic numbers of the species of *Leucojum* consist of 7, 8, 9 and 11, and the basic number of *Galanthus* is 12.

The *Leucojum* species distributed in the south west have the smallest basic numbers and gradually as the species are found farther north the basic number increases from 7 to 8, then to 9, and eventually in *L. vernum* and *L. aestivum* to 11.

Darlington (1946) has shown how in *Fritillaria* and *Lycoris* the evolution of the chromosome numbers occurs. In *Fritillaria* the basic chromosome number of most species is 12 but in *F. ruthenica* the basic number is 9 which has occurred by the reciprocal process of fusion, and *F. pudica* with a basic number of 13 shows a gain by fragmentation.

The idiograms of the 3 Fritillarias appear thus :—

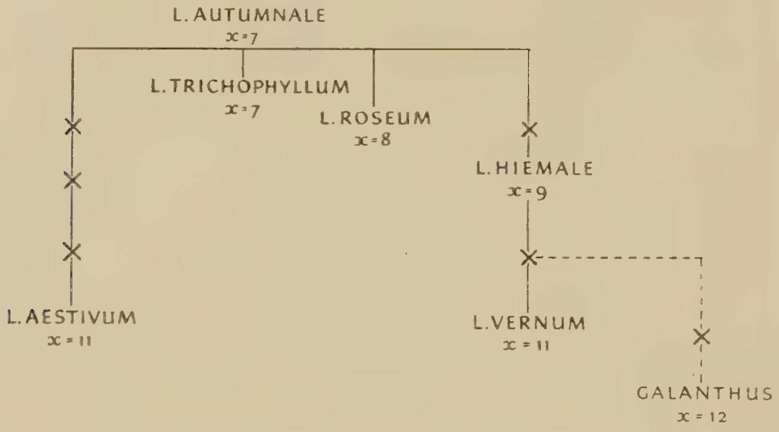
F. ruthenica	Λ Λ	Λ Λ	Λ ʌ ʌ	ʌ ʌ	x=9
F. meleagris	Λ Λ	ʌ ʌ ʌ ʌ	ʌ ʌ ʌ ʌ	ʌ ʌ	x=12
F. pudica	Λ ʌ ʌ	ʌ ʌ ʌ ʌ	ʌ ʌ ʌ ʌ	ʌ ʌ	x=13

The same form of fragmentation appears to occur in the two *Leucojum* species *L. hiemale* (2n=18) and *L. autumnale* (2n=14).

L. autumnale	Λ Λ	Λ Λ	ʌ ʌ ʌ'	x=7
L. hiemale	Λ Λ	ʌ ʌ ʌ ʌ	ʌ ʌ ʌ'	x=9

The idiogram of *L. autumnale* differs from that of *L. hiemale* by the latter lacking 2 pairs with median centromeres and gaining 4 smaller pairs with terminal centromeres. If the 2 pairs with median centromeres of *L. autumnale* broke into 4 pairs with subterminal and nearly terminal centromeres the idiogram of *L. hiemale* would be created. The idiograms are taken from the work of J. Barros Neves (1939).

If one takes into consideration the external characters, the numbers of the chromosomes and their shapes at mitosis and the geographical distribution, it is possible to speculate how the evolution of the different species occurred. The diagram is based on the assumption that the changes of the chromosome numbers have been solely by increase.



Church (1908) and other writers have drawn attention to the close morphological resemblance between *L. vernum* and species of *Galanthus*; further, the sequence of chromosome basic numbers from 7 to 11 in *Leucojum* and 12 in *Galanthus* suggests that *Galanthus* might be descended from some *Leucojum* species. But if the geographical distribution of the two genera is considered on the map, it is clear that the largest number of different species of *Leucojum* are congregated in the western Mediterranean area and the largest number of different species of *Galanthus* are congregated in the Caucasus and Asia Minor. Vavilov (1926 and 1930) suggested the theory that ‘ the centres of diversity ’ are ‘ the centres of origin ’. If this theory is accepted it would appear that in the Glacial Period when the flora of northern and central Europe was in all probability mostly destroyed (Seward, 1945) the *Leucojum–Galanthus* ancestral types were driven down from central Europe to Spain, Portugal and North Africa in the west, and to the Caucasus and Asia Minor in the east. From these two ancestral types there might well have evolved the genus *Leucojum* in the west and the genus *Galanthus* in the east.

Gradually as the chromosomes of all the different genera are known and maps are made, the phylogeny of plants may become clearer. Dr. Darlington has attempted to show the origin of all woody families of Angiosperms and Gymnosperms from a basic number of 7 chromosomes.

We are only on the threshold of this line of research which I suggest may be of great assistance to the study of taxonomy.

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Dr. S. C. Harland said that he would have to approach the subject from the point of view of one who was largely ignorant of general taxonomy. He had, however, worked on the genus *Gossypium* for many years, and had helped to use the data of both cytology and genetics in formulating a revised classification which took the data of these two disciplines into account.

The first point that struck one was the fact that the earlier taxonomists were so often right in their classifications; how few were the mistakes which they made. They had gone wrong on some points, however. At least two species which they had assigned to other genera had had to be incorporated in the genus *Gossypium.* This was the case with *Erioxylum aridum*, now known as *Gossypium aridum*, and with *Thurberia thespesioides*, now known as *Gossypium Thurberi.* At least two other species were assigned to new genera since not only was the basic chromosome number different from all the other known species, being 12 instead of 13 pairs, but also because they would not graft on other species of *Gossypium.* He was inclined to attribute great importance to grafting relationships though the use that could be made of them varied from Order to Order.

To sum up, he thought that while without the aid of cytology and genetics the taxonomist could make logical classifications of real validity, the final polish in many cases would perhaps have to be given by cytological and genetical data.

Professor T. G. B. Osborn said that he had been interested to note in Dr. Turrill's opening remarks that he included the cytoplasm amongst the cytological features to be considered by the taxonomist. He, too, felt that the importance of the extra nuclear constituents of the cell was sometimes in danger of being overlooked because of the great advances in karyology and structure of the chromosomes. Dr. Harland's remark that a useful guide to affinity between plants was sometimes to be gained from their ability to form grafts seemed to him to stress the importance of the cytoplasm and the compatibility of its proteins.

Dr. Turrill had pointed out that, whilst in some genera a common basic number of chromosomes had been recorded with or without polyploidy, in others the chromosome numbers were much more variable. Mr. Smith White in a recent paper in the *Proceedings of the Linnean Society of New South Wales* had confirmed the number $n=11$ for six additional species of *Eucalyptus.* Atchison has recently found this number in all but two of 36 species examined. These two, Smith White feels, should be examined from wild material. On the other hand, in a second paper published in the same part of the *Proceedings*, Smith

White records his findings in the Epacridaceae, a comparatively small family of characteristic habit. In the tribe Styphelieae the haploid number is very variable. In species of *Leucopogon* counts of $n=4, 6, 10, 12$ and 24 were recorded. In allied genera, some of which had been at times included with *Leucopogon*, in the original big genus *Styphelia*, counts of $n=7$, 8 and 9 were also obtained.

No doubt such a diversity of numbers was explicable by some such ingenious scheme of breaking (or union) of chromosomes and gain (or loss) of centromeres as Colonel Stern had developed for *Galanthus* and *Leucojum*. Indeed, Mr. Smith White had attempted something of the kind. But in view of the existence of such diversity within a single genus, it appeared desirable to be careful in stressing the importance of mere numbers of chromosomes as a guide to taxonomic affinity.

Dr. D. H. VALENTINE said he had two points to make. First, some speakers had referred to ways in which chromosome numbers might change. In this connection, it was worth drawing attention to the work of Babcock and his collaborators on the genus *Crepis*. There is strong evidence that a reduction in number, e.g. from $n=4$ to $n=3$, has been due, in some species of *Crepis*, to processes involving reciprocal translocation ; such changes have probably occurred more than once in the evolution of the genus.

Secondly, he wished to draw attention to some of the taxonomic problems which arise in connection with polyploidy. In recent years, several examples of polyploid (probably autoploid) forms which differ in only slight morphological details or not at all from the related diploids, have been described, e.g. in *Rumex acetosella* L. by Löve and in *Valeriana officinalis* L. by Skalinska. In such cases, identification by ordinary taxonomic methods is difficult ; and the term ‘ chromosome races ’ has sometimes been used to describe the forms. In his opinion, this was wrong ; where, as in the examples quoted, the forms are genetically isolated from one another and have distinct geographical and ecological ranges, the use of the term ‘ species ’ is justified. Reliable diagnosis of such species, even of herbarium material, is often possible if characters such as pollen grain size and stomatal index are used.

Mr. F. C. GRIGG : The study of karyology, rather than of the more comprehensive cytology, by certain classes of students and especially by those concerned with plants, depends largely on previous training. While it is undeniable that the chromosomes are of prime importance to the systematist, much information can be gained by a study of extra-nuclear cytology. The plant cytologist usually has a horticultural background whereas the animal cytologist often starts off with a medical education. The latter has a quite different conception of the characters of the material he handles and views them from a functional standpoint. The diversity of tissue is greater and the chromosomes are usually the less conspicuous of the cellular organellae, and he does not confine himself to but three kinds of tissue as does the botanist, e.g. the root-tip, the pollen and the embryo-sac mother cells. Only in recent years have botanists shown serious interest in plant embryology, while with animal histologists embryology has long been studied. Plant tissue culture is also very modern.

It would be profitable for plant cytologists to study living tissue by different observational methods, and, of these, dark-ground illumination is one of the most valuable. When properly used on suitable material the dark-ground illuminator will provide an entirely different picture of the cell and serve as a modifying influence on other studies. The phase-contrast microscope also offers valuable opportunities towards this end and is exceedingly useful for work on permanent mounts in suitable media.

Mr. L. F. La Cour: There is no justification for the claim that the methods employed by animal cytologists are superior to those used with plant materials. The Feulgen squash method which involves the use of relatively high temperature, compares favourably with any other known method. It is highly esteemed by plant and animal workers alike. The phase-contrast microscope for the study of chromosomes in plant cells is useless owing to the thickness of cell walls.

Dr. J. Ramsbottom: I strongly support Dr. Turrill's plea for closer co-operation between taxonomists and cytologists. Indeed, I would go much further and say that it is to the general benefit of all branches of botany to co-operate to the full, and in particular for taxonomists to search in other disciplines for facts that may be used in their aims to identify, classify and learn the nature of the units with which they work. Mycologists have had forced upon them many aspects of the advantages that result from such collaboration.

Mycology has not anything to add at present on the lines of the researches especially under consideration to-night. On more than one occasion over the last quarter of a century I have pointed out that in the different branches of Natural History the methods are bound to differ because of the material to hand. To take the two extremes, a species in palaeontology is a different entity, though not necessarily a different concept, from that in bacteriology.

We have to deal with material available. The herbarium botanist is often criticized because he works with dried specimens. It is like criticizing a palaeobotanist because he deals with dead specimens, or an anatomist because he uses pickled material. The amazing thing is the amount of information a systematist in flowering plants can gain from pressed specimens. Now a taxonomist should welcome any additional information no matter whence. Cytology is only morphology writ small. The morphology, number, etc., of the chromosomes is as much a taxonomic character as any other.

Many of the more recent ' new looks ' of the flowering plant systematist have had their vogue in mycology for very many years. Cytology, which was formerly the fashion of the academies, has, however, fallen into some disfavour because, owing to the usual small size of the nuclei, the niceties of nuclear behaviour can rarely be followed. A controversy about the nuclear divisions in the ascus and the possibility of a double fusion has lasted now for forty years. What one might designate gross cytology has, however, proved very fertile in results.

The basic fact that in the life-cycle of many fungi there is a stage in which cells have a single nucleus and one in which they are binucleate with conjugate division and eventual fusion is of fundamental importance: it is tied up sometimes with the phenomenon of heterothallism. Occasionally, where fructifications are formed, there is only one (uninucleate or haploid) strain. Thus in many Agarics there are species which sometimes show four spores on the basidium, sometimes two. At one time these were thought to be unrelated and Maire founded a genus *Godfrinia* on a form of *Hygrophorus conicus* with uninucleate cells in the sporophore and a bi-spored basidium. It is now known that this and similar forms, some of which have the spore from the one type of basidium much larger than from the other, are really fruiting uninucleate forms. Many such bi-spored basidial forms are now known, and the realization of their occurrence has cleared up many puzzles in mycological taxonomy.

Data about nuclei prove useful in all kinds of ways. Thus *Neurospora sitophila* has eight uninucleate spores in the ascus and is heterothallic, whereas *N. tetrasperma* has four binucleate spores and is homothallic. In the latter it is known that normally the nuclei in a spore are of opposite sign or compatability, hence the homothallism.

Other points where a knowledge of nuclear behaviour proves of value is in the so-called dual phenomenon where differences in strains of some fungi with multinucleate spores is related to the number of nuclei present; and in the grafting of mycelia of different species and strains.

Professor W. H. PEARSALL, in conclusion, pointed out that he thought the discussion had shown that the study of cytological detail had placed in the hands of taxonomists something which at times proved to be a powerful new weapon, although the results were not always easy to interpret and at present appeared to be of greater interest to botanists than to zoologists.

PROCEEDINGS OF THE GENERAL MEETING ON
24 March 1949

Professor G. R. DE BEER, F.R.S., President,
in the Chair.

The Proceedings of the General Meeting held on Thursday, 10 March 1949, having been circulated, were taken as read and confirmed.

The President announced the award of this year's Linnean Medal to Professor D. M. S. WATSON, F.R.S. Linnean Medals have also been awarded to Dr. W. T. CALMAN, C.B., F.R.S., and Professor F. E. WEISS, F.R.S., in respect of the war years during which no awards were made.

The following were thanked for gifts made to the Library since the last Meeting:—Mr. B. C. Adkin, Mrs. Vera Higgins, V.M.H., Dr. A. C. Moule, Lieut.-Col. R. B. Seymour Sewell, C.I.E., Professor James Small, Dr. J. K. Spearing and Mr. B. Verdcourt.

The following Fellow signed the Obligation in the Roll and Charter Book, and was admitted a Fellow:—Mr. John Anthony, M.C., M.A., B.Sc.

The President reported the death of Mr. John Ardagh, A.L.S.

Certificates of recommendation for election to Fellowship of the Candidates named in the Agenda of the present General Meeting were taken as read for the first time, and the following additional certificates were read:—Frances Ethel Ince, M.Sc., Charles Adrian Hopkins, B.Sc., Eleanor Mary Ord Laurie, M.Sc., Christopher Albert Walter Sandeman, Dr. Frederick James Fitzmaurice Barrington, F.R.C.S., F.R.C.P., and Surendra Rohatgi, B.Sc. (See p. 150.)

Read for the first time a certificate of recommendation for election to Foreign Membership, in favour of Professor Dr. OTTO JAAG, of the Eidgenossische Technische Hochschule, Zürich.

Read for the first time certificates of recommendation for election to Associateship *honoris causa*, in favour of Dr. ROBERT LLOYD PRAEGER and Dr. ARVID HJALMAR UGGLA, R.N.O., R.V.O.

In accordance with Chap. 10, Sect. 8 of the Bye-Laws, the following Fellows were elected, by show of hands, as Auditors of the Treasurer's accounts for 1948–49 :—

Representing the Council : Mr. A. H. G. Alston.
Mr. H. W. Parker.

Representing the Fellows : Mr. I. H. Burkill.
Miss E. M. Wakefield.

A Discussion on Animal and Plant Populations in Fresh Water was opened by Dr. T. T. Macan and Mr. D. Le Cren, Freshwater Biological Association, Wray Castle, Ambleside, with the following papers :—

Dr. T. T. Macan. Factors limiting Freshwater Populations.

Mr. D. Le Cren. Interrelationships between Population, Production and Growth Rates in Freshwater Fish Populations.

(In the ensuing general discussion, the following took part :—Professor W. H. Pearsall, the President, Dr. G. S. Carter, Miss M. E. Brown, Dr. W. Rushton, Dr. E. Trewavas, Major Maxwell Knight, O.B.E., Mr. F. C. Grigg ; Dr. Macan and Mr. Le Cren replied.)

DISCUSSION ON ANIMAL AND PLANT POPULATIONS IN FRESH WATER

FACTORS LIMITING FRESHWATER POPULATIONS

By Dr. T. T. Macan, Freshwater Biological Association.

A great many collections of bottom samples with grabs, and of plankton with nets have been made, but I do not want to talk about that aspect of population, which may be described as the static aspect. I wish to discuss the dynamic aspect, about which very little is known.

As a starting point we may take one of those food chain diagrams which appear so often in books and pamphlets, remarking that details of any chain have never been worked out. The total quantity of vegetable matter, whether planktonic algae, higher rooted plants, or epiphytic algae will depend on the supply of nutrient salts and the depth to which light penetrates. This is the basis of the food chain and the point from which I wish to start. Every successive link in the chain converts about 1/7 of what it eats into living tissue ; this figure of 1/7 is a rough approximation, for there are no exact data for fresh water, but that is not important for the development of the present argument. Theoretically the amount of life produced at any one link should depend on the amount of vegetable matter and the number of links intervening ; i.e. carnivores feeding on the carnivores which feed on the herbivores should amount to 1/7 of 1/7 of 1/7 of the quantity of vegetable matter available. In practice this theoretical maximum is not achieved and I want to examine the usual reasons why not.

First a digression to point out that if fish production alone is discussed, the most important factor is the amount of lake bottom shallow enough for plant growth. The char and some coregonids are the only British fish to feed regularly all through life on plankton, though the trout may do so in exceptional circumstances. The trout and the coarse fish feed mainly on the invertebrate fauna in shallow water. A deep lake with steep sides will, therefore, be unproductive of fish, except char. Some fish, the perch for example, feed on plankton when they are tiny and turn to littoral fauna when they are larger. In a deep, steep-sided lake the young stages find abundant food supply and a great number survive ; but there is insufficient food in the narrow littoral region for the larger fish which result. I am now in Mr. Le Cren's territory and must break off.

To revert to the three main factors preventing maximum development of the food-chain, they are :—

(1) excessive cropping ;
(2) catastrophes ;
(3) presence of inhibitory substances.

1. *Excessive cropping* is probably the most universally important of the three factors. Inhibitory substances may be a widespread cause of poor populations in waters deficient in dissolved substances, sweeping away by flood is certainly important in rivers of a certain type, but excessive cropping is a factor almost everywhere. The outcome of fishery research is usually a regulation defining the lowest size of fish which may be caught, the purpose being to give every fish a chance to breed so that the maximum exploitation of the species may be achieved. Presumably the same principle applies all down the food chain and is particularly important in fresh water where so many animals breed but once during the year. Fresh water is peculiar too in what appears to be an adaptation of the predator. It is a general principle that carnivores have catholic tastes and range far afield, turning their attention to something else if one particular species gets scarce. A fish has much less scope for wandering far afield when food gets short. But shortage of food affects it less seriously than other animals. These have a certain adult size fixed within rather narrow limits and, though starvation may produce a stunted specimen, in general, if food is insufficient for growth to full size, it is insufficient for life at all. But, if a fish is short of food, it merely fails to grow, and a sexually mature, apparently normal fish, may be many times smaller than another living in better conditions. This must lead to a very severe pressure on the food organisms ; they get no opportunity to develop to the maximum of their capacity and probably the species composition of the population is affected as well. But hitherto this line does not seem to have been investigated.

2. *Catastrophes.* Excessive drought, heat, or cold affect aquatic animals much less than land animals. During a warm still spell or a long period under snow-covered ice, decomposition may use up all the dissolved oxygen and destroy the fauna. But this is an exceptional occurrence. In rivers with impermeable gathering grounds, that is, all rivers flowing off the mountains of Wales, Scotland, the Lake District, and the Pennines, the effect of sudden floods is of major importance. Pentelow, in the classic study of the River Tees, opines that the liability to sudden floods is the cause of the poor fauna, though he was unable to devise a means of measuring the magnitude of the effect. Butcher, of the same team, records that *Cladophora* usually made its appearance in May in a stretch below the inflow of a polluted tributary and gradually attained great luxuriance, providing food and cover for a rich assemblage of animals. By July it was so thick that it was unstable and the first flood swept it away ; and it was not seen again till the following year.

3. *Inhibitory substances.* These may be important in waters poor in nutrient substances and from the point of view of scientific research this is probably the most important of the three factors. There has been much discussion about the poverty of waters where humus substances are present, but doubt has often remained whether the poverty is due to toxic substances or merely to deficiency in some essential nutrient. But in Lake District lakes the development of vegetation in regions where little silt falls to the bottom leads to a stage where sterile patches are frequent. There can be no doubt that plant growth is actively inhibited by some substance formed in the soil.

Nauplii of *Artemia*, the Brine Shrimp, will hatch in NaCl in a concentration of 0·01–3·5 molar and in a pH of about 2–13. But potassium is surprisingly toxic, and there is no development in quite low concentrations unless there are more than 9 parts of Na to 1 K. There is some evidence to suggest that *Gammarus pulex* will not survive if the proportions of Mg and K to Ca and Na exceed a certain threshold.

Lead is toxic to some animals in a concentration of 1 part in 10 million and rainwater seeping through old lead-mine washings may affect a stream fauna for years after mining has ceased. Pollution is not within the scope of this talk but it seems possible that a concentration as low as this might be given by some natural rocks.

Sir Malcolm Watson noticed that places with an iron deposit did not harbour mosquito larvae. His explanation is that water seeping out of the ground contains ferrous iron which is oxidized to ferric iron on contact with the air. This comes down as an insoluble floc and carries with it the micro-organisms on which the mosquito larvae feed. The waterworks engineer uses a not dissimilar technique to get rid of algae.

Limnaea pereger is a remarkably ubiquitous pond snail. It is absent from 8 out of 40 Lake District tarns. Five of these are those with the lowest calcium concentration and the remaining three are all in woods. A fourth woodland tarn has very few *L. pereger*. The rest of the fauna gives the impression that these tarns are richer than most and it appears that the absence of *L. pereger* must be due to some substance unfavourable to it. Its ecological niche is not taken by any other animal as far as can be seen.

THE INTERRELATIONSHIPS BETWEEN POPULATION, PRODUCTION AND GROWTH-RATE IN FRESHWATER FISH.

By E. D. Le Cren.

Freshwater Biological Association, Wray Castle, Ambleside.

(With 3 Text-figures.)

Dr. Macan has spoken in general of the utilization of one link in the food chain by the next. I want to take one link in particular—that of fish eating fish food (bottom fauna or plankton)—and discuss it in more detail, particularly in relation to the total production of fish, their population density and growth rate. It will, I am afraid, be rather a theoretical and speculative discussion, though I hope that it will be somewhat provocative.

It will be convenient to start by defining our terms and briefly indicating their inter-relationships. These can be shown diagrammatically (Fig. 1). The *population* is increased by *reproduction*, and decreased by *mortality*. Population in its turn affects the *growth rate*. Growth is derived from the *food* eaten, much of which, however, is used in the *maintenance* of the fishes' bodies. The product of growth and population is a measure of the *production* of fish. This term is used here as defined by Allen (1946), Ricker and Foerster (1948), Ivlev (1945) and other workers, as the 'total quantity of fish flesh grown' during a given period, regardless of its ultimate end, or whether all of it survives to the end of the period under consideration.

The production is subject to 'utilization' by all the factors that cause *mortality* to the population. These can be classed in three groups:—*fishing effort* by man, which gives rise to *yield*, *predation* which leads on to the next link in the food chain, and *death through disease and physiological causes*. Another term not present on the diagram is 'standing crop'. This can be defined as the total weight of fish present at any particular time.

The production of fish as compared with the production of fish food is the best measure of the efficiency of this link in the food chain. There is, as far as I know, no measure of this efficiency under any natural conditions. Efficiencies of up to 35 per cent or one-third have been obtained experimentally, but it is very unlikely that efficiencies approaching this ever occur naturally.

There are two instances where the production of fish in a natural environment has been estimated. Ricker and Foerster (1948) have recently published estimates of the production of the fry of the sockeye salmon (*Onchorhynchus nerka* Walbaum) in Cultus Lake, British Columbia, over a period of twelve years, and Allen (1946) has published a progress report on an investigation into the brown trout (*Salmo trutta* L.) population and production in the Horokiwi River in New Zealand.

There is not time to go into the details of these works, but for those who do not know the experiments at Cultus Lake, I will briefly describe them. The sockeye salmon spawn in the afferent streams just above a lake, when the fry hatch they make their way into the lake and spend, in most cases, nearly a year in the lake feeding on zooplankton and growing. They then migrate out of the lake to the sea to return about four years later as spawning adults.

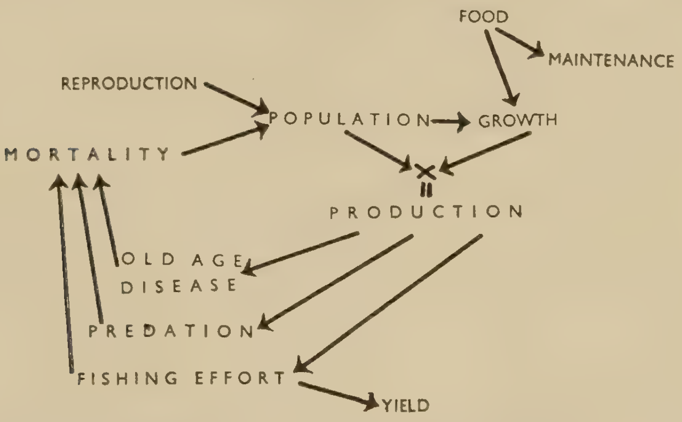

Fig. 1.—Diagram illustrating the inter-relationships between population, growth and production in fish, and the factors affecting them.

At Cultus Lake all the adults were counted into the lake and all the fry counted out. Limnological investigations were made on the lake, and estimates of mortality in the fry made by releasing tagged fry at various times throughout the year and checking their recapture when they migrated. The growth and food of the fry was traced throughout the year from samples taken from the stomachs of predatory fish. There is a four-year cycle of abundance of sockeye salmon, so the population of fry varied considerably. The annual production was obtained from the product of the average population and growth rate, estimated for every half-month, and summed over the year.

The annual production ranged from 4,850 to 40,700 kg. (10,700–90,000 lb.). The latter is a production of 66 kg. per hectare (56 lb./acre). Six of the years had a production between 4,850 and 7,130 kg. (10,700–15,800 lb.) with lower population densities. Six years, however, had higher production with usually higher population densities. Figure 2 is a graph of the relationship between initial population density (actually the number of eggs spawned) and production, and a second graph showing the production plotted against the final population. As there was a very high and somewhat variable mortality during the year, it is not easy to give an 'average' population density over the year. (The crosses on these graphs are for years after predator control, which may have affected the relationship between production and population. For the purposes of the present argument they can be ignored.) It will be seen from these graphs that when the population density was low, production was also low, and there was no very definite relationship between the two, though production tended to be greater with a higher population. The higher populations, however, gave rise to a higher production, but there appears to be an upper limit, when an increase in population would not give rise to an increase in production.

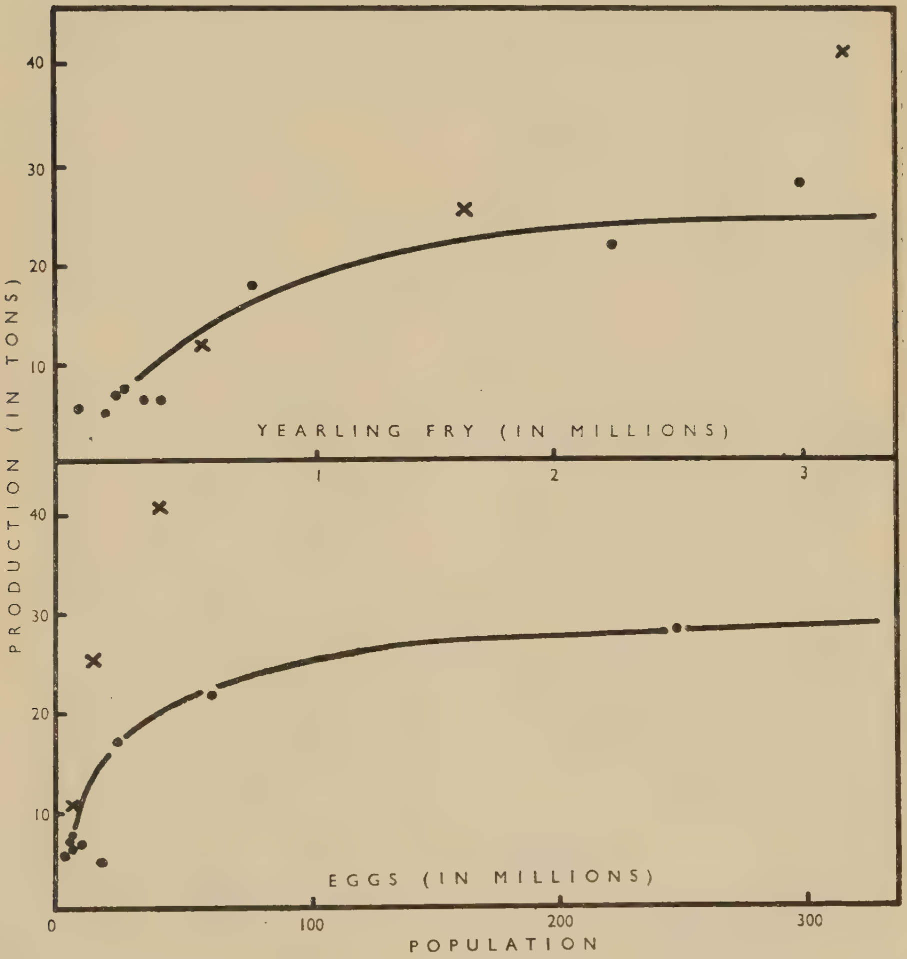

FIG. 2.—Graphs showing the relationship between population and production for young sockeye salmon in Cultus Lake. Dots indicate years before, crosses years after, predator control. Drawn from data published by Ricker and Foerster (1948).

If the figures for the average weight of migrating fry each year are examined (Foerster, 1943), it is found that at low populations there was no very definite relationship, but at high populations there is a definite inverse correlation between population and average fish size.

It was not possible to obtain data on the plankton food supply adequate to correlate with production, but approximate figures for four years would suggest that the plankton production varies much less than the population of salmon fry. There was evidence that in years of high fry population the plankton decreased more rapidly after the summer maximum (Ricker, 1937).

From data on stomach contents Ricker estimated that in the year of a production of 40 tons of sockeye, they consumed 150 tons wet weight of plankton, though this may be a conservative estimate. This would appear to be about the maximum possible consumption of fish food.

From these interesting figures it may be possible to draw a few conclusions. It would appear that at the lower levels of population—or more accurately spawning—the salmon did not utilize nearly all the production of plankton ; with increase in population density, however, the food supply becomes limiting to the weight of salmon produced. As within fairly wide limits the final size and growth rate can very considerably (the unusual peculiarity of fish mentioned by Dr. Macan) this weight of salmon, the maximum production, could consist of a large number of smaller fish or a smaller number of larger individuals. It is possible, however, to conceive a situation in which the initial population might be so dense that less than the maximum production would be achieved ; and, as Dr. Macan has pointed out, this probably occurs in many natural environments.

The data of Allen (1946) for trout in the Horokiwi River are as yet for only two years. He shows, however, a graph of size of fish and population density throughout the length of the stream and points out that it indicates that there is no correlation between density and growth rate. This would suggest that food supply is not a limiting factor to growth or production at that population level. (The rate of production is estimated at 7,000 lb. or about 800 kg./hectare (680 lb./acre), which is more than ten times the maximum for sockeye in Cultus Lake.)

These data might indicate that, in fact, in some fish populations, the low efficiency of fish production from the production of fish food may be due more to too low a population of fish than to too high a population. It would also suggest that when the population is considerably lower than that which will make full use of the food supply, there is no inverse relationship between population and growth rate. There is, however, no reason to suppose that this is the case in every environment, and in fact there is evidence from several sources that in many cases over-population may occur. Several experiments are on record where slow-growing fish populations have been heavily fished, and where the reduction in population has led to a marked increase in growth rate (e.g., Dahl, 1919). The growth rate, and possibly production, in these instances being severely affected by over-population ; other cases are also on record, however, where the hoped-for increase in growth did not occur. In Windermere, for example, we have fished the perch (*Perca fluviatilis* L.) population heavily each year since 1941. The fall in catches indicates that the population has now been less than 10 per cent. of its 1940 level for four years, but there has been hardly any indication of increase in average growth rate. All this would suggest that in this and some similar cases the food supply was not limiting production or growth rate.

Experimental work on growing fish in the laboratory (particularly the work of Brown on trout (1946)) has indicated that another important factor may be at work in the utilization of food supply by fish. Part of the food of fish is used for maintenance, and above a certain size this is probably proportional to the size of the fish, but any food eaten in excess of maintenance requirements is utilized for growth. The over-all efficiency of utilization of food for growth will thus depend upon the total quantity of food available—how much greater this is than the basic maintenance requirement. It has been found, however, that with increase in the amount of food available for growth, the efficiency of its utilization falls. Thus, while a very dense population eating only about 1 per cent. of its weight per day and growing relatively slowly will have a low over-all efficiency of utilization (perhaps as low as 1 per cent.), a population which is dense enough to have a somewhat restricted food supply, and eats say 2 per cent. of its weight per day, will have an over-all efficiency (up to 30 per cent.) as great or greater than a population with unrestricted food supply (eating say 4 per cent. of its weight per day). Thus, above a certain level any increase in food supply leads to hardly any increase in growth rate.

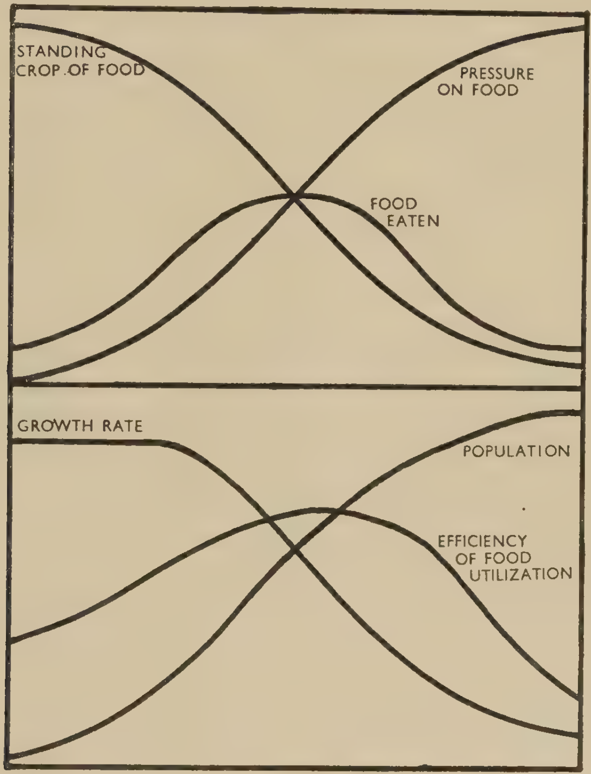

FIG. 3.—Diagram summarizing a possible form of inter-relationship between food, population and growth rate with different population densities of fish.

When a population of fish is very dense it may have a reduced production, because, as Dr. Macan has pointed out, it may over-crop the food supply and reduce the population of food animals below the level at which they give the greatest production. The over-cropping of food supply by the fish is exactly analogous to the over-fishing of a fish population by man. The density of the population of fish is equivalent to the 'fishing effort' of man, and just as the 'yield' does not increase but may decrease when a certain fishing effort is exceeded, so the supply of food available to a fish may decrease if the fishes' population becomes too dense.

We may perhaps sum up all these operating factors in yet another diagram (Fig. 3). With increase in population the pressure on the food supply increases, leading to a reduction in its standing crop. The actual consumption of food will rise to a maximum and then decrease again as the food supply becomes severely depleted. As the population increases, increase in food eaten and increase in efficiency of its utilization will maintain a high growth rate. With higher populations, however, the growth rate will fall and the efficiency of utilization will fall as the quantity of food available in excess of maintenance requirements falls as well.

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GENERAL DISCUSSION.

Professor W. H. PEARSALL spoke as one who represented the standing crop of food on which the animal populations depended. He pointed out that in spite of the importance which had always been attached to the phytoplankton as an element in productivity there was no real evidence that the animal population made any serious inroads on this part of the plant population. The growth curves of microscopic free-floating plants in nature resemble those obtained in isolated nutrient cultures, no reduction in numbers due to cropping being observed. The diminishing numbers of the plankton plants appeared to be associated mainly with diminishing supplies of mineral nutrients or to catastrophic epidemics caused by a fungal attack.

Concerning attached plants on the shores, the principal change taking place in this plant population appeared to be that due to the loss of soil bases, particularly lime, which results from plant growth so that sterile soils are produced, rich in iron and organic matter on which few plants can grow and from which animals seem to be frequently absent.

The third point of view which should be emphasized was that as soon as mud accumulates on a lake shore, organic matter also accumulates in it and it becomes deficient in oxygen. It is thus only possible for animals (chironomids and pisidia) which have special respiratory pigments enabling them to absorb oxygen from low external concentrations to live on it. Thus in this habitat the larger animals are usually scarce, and the bulk of the animal population lives, as it were, raised above the mud on the larger plants which may be found thereon.

The PRESIDENT agreed with Professor Pearsall and said that he had been very struck with the effect on Swiss lakes of the diversion of sewage into them. The increase in organic matter had been followed by a great increase in the phytoplankton which, while it lived, provided abundant oxygen in the superficial layers of water. But when it died and sank, the decomposition of this plankton robbed the water of so much oxygen as to form zones of asphyxiation for the fish. He felt sure that Dr. Macan would agree to add to the factors which he enumerated as controlling the population of fish the local absence of oxygen.

Dr. W. Rushton : The vast difference between rivers, lakes and storage waters in different parts of the country makes it difficult to follow out the links in a food chain.

Rivers : Consideration of a few rivers where the links in the food chains seem to fit in very well and lead up to trout which reach an attractive size and shape, would mean taking the upper parts of a river like the Test in Hampshire, a stream arising from springs in the chalk, whose waters are clear, free from pollution, producing very active fish, attractive to the eye and of reasonable size. In such a stream, with a fairly fast flow, not subject to flooding as is a mountain stream, one can trace the links in the food chain right up to the fish.

Following the seasonal changes over several years, with a colleague, Dr. H Slack, in daily contact with the stream, in broad outline we found that the diatoms became active very early in the year, some years as early as February, the dominant form always being *Melosira* which appeared on the clean gravel and adhering to water weeds such as *Ranunculus fluitans*.

The diatoms seemed to form the principal food of caddis fly larvae, which become very evident in the early part of the year, whilst around the roots masses of the fresh water shrimp (*Gammarus pulex*) can always be found.

Mollusca such as *Limnaea pereger* do not thrive, due possibly to the fast flow ; odd specimens could be found in some of the stagnant side bays but one would not put this species among the food links in this stream.

About March or April, when the diatoms in addition to *Melosira* increase, certain unicellular algae increase, making many of the stones appear green ; at the same time certain protozoa and microscopic crustacea multiply, coinciding with the time the trout fry, having lost their yolk sac, are beginning to feed.

Multiplication of *Gammarus* seems to be stimulated along with the hatching out of some of the small insects of the Ephemerideae group, and the smaller *Gammarus*, together with the larval forms of the small Ephemerideae appear to be the food of year old fish.

In the early part of the year, the fish over a year old seem to feed largely on caddis larvae with some *Gammarus*, and later on *Gammarus* and aquatic flies, both larval and imagos. During the late spring and summer, minnows seem to become abundant and are taken by mature fish of say three years old and over. Crayfish do not appear in the Test as far as our experience goes. During the colder months of the year, the fish feed less, at some periods, even going off feeding for long periods. One gets similar conditions in the upper parts of the Kennet and Itchin.

Taking another case, the upper parts of the River Ribble, which rises from springs on the Pennines at an altitude of about 1,700–1,800 feet in wild moorland country at the border of N.E. Lancashire and the West Riding of Yorkshire (the source of the Yorkshire Ouse is in the same area).

During the first few miles of the Ribble, the stream is small, fast running in a somewhat deepish gulley, with large angular and smooth boulders in the bed of the stream and jutting out from the sides, with pebbles of various sizes down to sand.

During heavy rainfall the water level rises and falls within a few hours, yet on the downstream side of the boulders grow mosses. Very few rooted plants can maintain a hold, yet through the season diatoms and accompanying small sized fauna right up to fresh-water shrimp can be found, and trout from fry up to half-pound fish are present in good, healthy condition, although the stream is not more than a foot or so in width or more than a few inches to a foot or so in depth, with an enormous number of small waterfalls.

In Scotland there are other streams where one can work out the links in a food chain.

In situations such as this, as the fish grow to maturity they fall back down stream to deeper and slower flowing waters where the food supply is greater, where competition may be more keen and other factors interfere with the links in the food chain.

Water storage reservoirs: Sheets of water of this kind might be regarded as artificial lakes of recent origin, as compared with natural lakes such as are found in the Lake District. Storage reservoirs are made either by putting a dam across a valley through which a stream passes, or by building embankments and pumping water into them from artesian wells or from a river.

The object of the engineer is to have a narrow, deep reservoir rather than a wide, shallow one, with sides as steep as possible to limit as far as possible shallow areas where rooted vegetation may thrive and possibly give trouble to the successful working of the waterworks concerned. There are many to choose from, but two suffice to illustrate how the links in the food chains seem to be upset; both are well known to trout anglers.

Take one in North Wales, which serves as a water supply to a northern city. It has been made by placing a dam across a valley with a maximum depth of about 80 feet, steep sides, supplied with water by two mountain streams a few feet in width and a depth of a few inches. The streams are very stony, practically no weed, and such fish foods as are available are of the nature of caddis larva, stone flies, with lower forms of life in the form of the algae colouring the stones green, with accompanying protozoa and slightly higher forms of animal life.

In times of heavy rainfall, the streams bring down a certain amount of silt which settles at the mouth, increasing the shallows and encouraging rooted weeds to grow.

The small size of the rivers is not sufficient to keep the reservoir stocked with trout, so other means are adopted. The bulk of the reservoir is too deep for rooted plants to extend far into it, and the trout are dependent for food on crustacea such as *Daphnia*, larvae and imagoes of aquatic insects like gnats, and insects which may alight on the surface, plus a few minnows.

The fish at maturity do not attain to such a weight as in, say, a limestone stream or a chalk stream.

Another reservoir in the South-West of England, which draws its water from an area where there is a more calcareous substratum with more shallows and more complete links in the food chain, produces fish of greater weight, but again artificial stocking has to be done.

In regard to growth rate and numbers of fish, two out of many known cases can be taken in support of what Mr. Le Cren has said.

Investigations carried out on six small lochs on the Isle of Islay in 1947 revealed that all six of them carried very clear water with rooted vegetation ranging from *Myriophyllum* up to water lilies with very little algae, the water supply was only rainwater and drainage from a few acres of sheep-grazing land. The geological formations show local patches of limestone; so far as purity of water is concerned, they were ideal trout waters.

The depth of the largest loch varies from a few inches to about ten feet, not too deep for rooted plants to flourish and, in fact, a certain amount of weed cutting has to be carried out in one loch owing to excessive growth of the *Elodea* introduced some years ago with the idea of improving the food for trout.

The trout present, when mature, are thin but of good colour; a few big fish are caught at times which appear to have been fed on Mollusca, *Limnaea pereger*, which is abundant in some of the shallows, and, possibly, on young trout. No shrimp could be found in the lochs.

These lochs had been stocked about ten times from areas in different parts of the British Isles, where the mature fish ran up to several pounds, and also with fish bred in a hatchery from eggs from many sources, yet the descendants in the course of a few years averaged the same weight. Reducing the numbers by netting made little difference, suggesting that limiting stock does not necessarily mean fewer fish of larger size.

The climate in this island is on the mild side, which indicates that there are other factors which play some part in affecting the growth rate.

Another example can be taken from a service reservoir which carries coarse fish, and where fishing is limited. Over a number of years the fish multiplied enormously with no increase in the food supply, resulting in increased numbers but smaller and weaker fish. During a spell of hot weather, fermentation of organic matter on the bed took place, decomposition gases such as sulphuretted hydrogen etc., were given off, and thousands of the weak fish died. There are factors which have not yet come to light which have a bearing on this population limitation.

To indicate how important the study of the living contents of fresh water with its economic bearing in regard to domestic water supplies, one might add the following :—

In an area in Essex not far from Colchester, a very shallow storage reservoir was completed about 1940. A very small brook enters the upper end, but the bulk of the water is pumped into it from the River Stour during those periods of the year when the flow is above a certain volume, which means that the supply is cut off in the summer months. The river drains a certain amount of cultivated land as well as passing through villages whose sewage effluents enter it. The ground over which it passes is clay and chalk so the water is on the high side for hardness. As a fishing stream, it seems more suitable for coarse fish than trout.

Before the reservoir was started and since storage has been done, regular chemical and biological studies have been carried out and weekly records kept. As the reservoir has been used for some seven to eight years it has been found that the sequence of seasonal diatoms etc., follows very much on the lines in other older sheets of water, but, after plotting the observations over seven years, by no stretch of the imagination can it be said that any two years coincide, neither does the chemical analysis of the waters clear up the obscure factors.

So far as higher plants are concerned, *Chara* has appeared and spread in some of the shallow areas, with a little *Elodea* and *Myriophyllum*, but in some years *Potamogeton pusillum* with its grass-like stems grows vigorously in one of the shallow bays. One would not regard this reservoir as a heavy algal one and no serious difficulty has occurred in regard to filtration ; possibly the reservoir is too young to have a reserve of plant requirements.

As regards fauna, in the early years Rotifers were fairly common, followed by the smaller Crustacea like *Daphnia*, *Cyclops*, with small Diptera and no *Gammarus*. The Mollusca found in the shallows are largely *Limnaea pereger*, *L. auricularia*, with large numbers of *Planorbis*.

The water pumped in has to pass through a screen with holes about one quarter of an inch in diameter, so that only small fish can get through. The small fish passing through are minnows and the fry of roach, perch and pike. Since the beginning of storage, the perch and pike have made good ; roach seem, however, to be playing a losing game. At present perch and pike seem to be competing for ascendency, the pike taking a heavy toll of perch during the early stages.

The problems in fresh water biology seem endless, and he would be a brave person who would generalize on all waters from observations in one area.

Major MAXWELL KNIGHT, O.B.E., said that some years ago he had the fishing in four ponds on a farm in Kent. Two of these ponds were very small and one contained only perch which never exceeded four inches in length, while the other pond held small roach. The perch pond had little or no vegetation but the roach pond was well supplied with plant life.

He netted the perch pond and took out upwards of 100 perch which he placed in the roach pond. For three years after this he caught and measured perch from each pond but there was no appreciable increase in size or length during that period. He mentioned that the roach pond was rather larger than the perch pond and did not originally seem to have so many fish.

Dr. MACAN replied to speakers as follows: Professor Pearsall has drawn attention to the different types of mud to be found on the bottom of lakes. If it were possible, it would be appropriate to mention at this point abundance of fauna in relation to type of bottom, but unfortunately it is not; and, although there are a great many records of numbers of animal per unit area in many lakes and the range is big, no correlation between numbers and type of bottom is possible on the data at present available.

Light penetration, an important factor in productivity in water, has been mentioned. In Ennerdale Lake in Cumberland the water is unstained with peat, has little mineral matter in suspension, and is poor in plankton, since the inflowing waters bring in little dissolved matter; plants can grow at a depth of 10 metres (30 feet). At the other extreme, in a cattle pond enriched by the dung of the animals which come to drink from it, sufficient light for plant growth does not penetrate more than a few centimetres.

It is well-established that trout in calcareous waters are generally large and those in lime-poor waters generally small, but it is disputed whether the cause is a direct effect of the water on the fish, or a richer food supply in calcareous waters. A good deal is known about what the fish feed on, but little about what the fish-food feeds on; detailed work on the food-chains is needed. A preliminary to work of this kind is identification of the organisms to species, which is not always possible, and much systematic work on the British fauna remains to be done. In this connection the speaker paid tribute to the Linnean Society's *Synopses of the British Fauna*, and hoped that the Society would press ahead with the project.

A further point raised by Dr. W. Rushton is related to the topic just discussed. The American workers have stressed that, if fish are to make good growth, they must be able to graduate to food morsels of ever increasing size, as they themselves grow. It is possibly significant that the larger freshwater organisms such as the large snails and the crayfish are found only in calcareous water.

Mr. LE CREN replied that it is always of interest to hear of the observations of anglers on fish populations, and the experiments sometimes carried out by them. These experiments often produce conflicting results; in some cases reduction of the population leads to an increase in individual size, in other cases the desired result is not obtained.

Mention has been made of the relative productivity of aquatic and terrestrial environments. From the practical point of view, some recent work in the tropics has shown that a much higher yield of protein food can be obtained from fish ponds than can at present be produced in the same regions by terrestrial animal husbandry.

PROCEEDINGS OF THE GENERAL MEETING ON 28 April 1949

Professor G. R. DE BEER, F.R.S., President,
in the Chair.

The Proceedings of the General Meeting held on Thursday, 24 March 1949, aving been circulated, were taken as read and confirmed.

The following were thanked for gifts made to the Library since the last Meeting :—Mr. Eric W. Baxter, Mr. H. H. Bloomer, Professor W. B. Brierley, Mr. K. C. Corsar, Professor F. E. Fritsch, Dr. J. J. Keevil, Mr. R. Morse, Professor F. E. Weiss, and the National Geographic Society, Washington.

The following Fellow signed the Obligation in the Roll and Charter Book, and was admitted a Fellow :—The Hon. David Bowes-Lyon.

Certificates of recommendation for election to Fellowship of the candidates named in the circulated ballot list were taken as read for the second time ; and recommendations in favour of Professor Arthur Roy Clapham and Leslie Francis Seamell Ward, M.A., were read for the first time. (See p. 150).

Read for the second time, a certificate of recommendation for election to Foreign Membership, in favour of Professor Dr. OTTO JAAG, of the Eidg. Technische Hochschule, Zürich ; and for the first time, one in favour of Dr. DAVID FAIRCHILD, of Coconut Grove, Florida, U.S.A.

Read for the second time certificates of recommendation for election to Associateship *honoris causa*, in favour of Dr. ROBERT LLOYD PRAEGER and Dr. ARVID HJALMAR UGGLA, R.N.O., R.V.O.

The President reported the deaths of Mr. John Humphrey Bell, Dr. Ananda Kentish Coomáraswámy and Mr. Herbert Stone, Fellows ; Professor August Weberbauer, Foreign Member ; and Dr. Vladimir V. Tchernavin, Associate *honoris causa.*

The following showed Exhibits :—

Professor G. R. DE BEER, F.R.S., P.L.S. Edmund Davall's Note Book.

Dr. MARGARET A. BRETT. New British records of Smuts on *Ulex minor* Roth.

Dr. R. BROOM, F.R.S. Plaster casts of specimens of hominoid Primates recently discovered in the Union of South Africa.

Dr. R. W. BUTCHER and Dr. N. REYNOLDS. A series of pure cultures of Algae.

Mr. G. J. CUNNELL. Twin sporogonia in *Polytrichum.*

Miss H. D. GARSIDE. Water-colour drawings of Cryptogams.

Dr. I. GORDON, for Mrs. E. W. SEXTON. The multiform species *Jassa falcata* (Montagu, 1808)—Crustacea, Amphipoda.

Mr. F. C. GRIGG. (1) An efficient device for examining and reading microfilms ; (2) Extra-Nuclear Cytology—results of recent researches ; (3) Macro-sections of entire human organs, lung, brain, etc., prepared by Prof. Gough and Mr. J. E. Wentworth, Welsh Nat. School of Medicine.

Dr. H. GRÜNEBERG, for Mr. P. G. LUTHER. Enzymatic maceration of skeletons.

Mrs. VERA HIGGINS. Water-colour drawings of *Crassula* species.

Mr. C. H. HOOPER. Insect visitors to fruit blossoms.

Dr. A. TINDELL HOPWOOD, Sec.L.S. Drawings of Antelopes, etc., by B. Waterhouse Hawkins.

Miss E. M. O. Laurie. (1) Mammalian clines associated with the rules of Bergmann, Allen and Gloger ; (2) A sub-species chain in *Peromyscus maniculatus* where the end forms overlap and do not interbreed ; (3) Two closely related species which overlap in their range but do not interbreed—*Apodemus sylvaticus* and *A. flavicollis.*

Dr. S. M. Manton, F.R.S. *Peripatus* : gaits and footprints.

Dr. W. J. Rees. Variation in *Purpura.*

Mr. S. Savage. Some remarkable handwritings in the Society's collections.

Dr. J. K. Spearing. (1) An aquatic Discomycete resembling *Ombrophila Clavus* (A. & S.) Phil. ; (2) A case of syncotyly in the common radish, *Raphanus sativus* Linn.

[Abstracts describing these Exhibits are printed below.]

Edmund Davall's Note Book.

By Professor G. R. de Beer, F.R.S., Pres., L.S.

The note book contains some of Davall's observations in natural history from 1783–88. The notes are entered in a copy of Daines Barrington's *The Naturalist's Journal* (London, 1775). The note book has been presented to the Society by Madame M. Hager-Davall, of Aarau. The text of the notes has been printed in *Proc. Linn. Soc. Lond.* **161,** pp. 56–63.

New British Records of Smuts on Ulex minor Roth

By Dr. Margaret A. Brett.

Ulex minor Roth has been found on various commons in south and south-west England, attacked by hitherto unrecorded members of the Ustilaginales, which perennate in the host plant. At flowering time the anthers of infected plants are coated with conidia of the smuts, and appear white and somewhat powdery, in contrast to the normal yellow colour. Spore balls (i.e., compound teleutospores) are formed later (*a*) in the essential organs of plants which show the systemic infection, and (*b*) in occasional pods and seeds on healthy plants. This latter infection has been proved by experiment to be due to the agency of insects, which collect conidia with pollen, and inoculate the stigmas of healthy flowers with the smut, at the same time as they pollinate them. The mycelium from this conidial inoculation grows down the style into the pods and there proceeds to the formation of spore balls. Pods on such secondary hosts invariably contain spore balls of more than one smut.

Demonstrations under the microscope, photographs, and cultures, were shown of three smuts obtained from this host.

The first is a ' covered ' smut, spore balls of which are formed in the seeds of white-anthered plants, and completely enclosed by the testa until maturity. Similar spore balls are also found in secondarily infected pods, replacing part or all of the contents of the seeds.

This smut grows moderately well in culture from single spore balls producing conidia which resemble those on the anthers of systemically infected plants. It will also eventually form new spore balls. These are characterized by the presence of a surrounding gelatinous zone which disappears at maturity—a feature of the genus *Sorosporium*, species of which have been recorded on leguminous hosts in Colorado, U.S.A.

Spore balls of another smut frequently associated with the first in secondarily infected pods, are larger, darker in colour, and mature more rapidly. A photograph showing the two together was exhibited. This smut grows freely in culture producing profusely budding conidia, which resemble those on the anthers of other infected plants. At spore ball formation (which will take place eventually in culture) no gelatinous investment is formed. This fact, together with the spiny exospore and characteristically prominent germ-pore, indicate that it is probably a species of *Thecaphora*, a genus which attacks leguminous, and other, hosts in this country.

The anthers of diseased plants containing small spore balls of a third smut were also shown. The mycelium of this attacks the pollen mother cells, so that no functional pollen is produced. The life history and identity of this smut fungus are being investigated.

Plaster casts of specimens of hominoid Primates recently discovered in the Union of South Africa

By Dr. R. Broom, F.R.S.

Dr. R. Broom exhibited casts of the more important of the finds of South African Ape-Men made during 1947 and 1948. The most important was the perfect skull of a female *Plesianthropus* found on 18 April and the pelvis discovered on 1 August 1947. The skull has a brain capacity of 482 cc, and though far below the human ranges of brain size, it is amazingly human in most points of structure. The pelvis is one of the most remarkable discoveries ever made. The ilium is so nearly human that some have suggested that it might be a human ilium that has got into the deposit. This would seem impossible, for we have over 150 teeth of *Plesianthropus* from this cave and not a single human tooth or any human bone. Further, though the ilium resembles that of man considerably, there are quite a number of important differences, and the ischium differs markedly in at least one character. The pelvis is manifestly not an anthropoid pelvis, being very unlike that of any known anthropoid ape.

A cast of a male *Plesianthropus* mandible was shown which has the canine and premolars and molars all ground down to one level as in man.

A brain cast of the female skull was shown, though this is not larger than that of some male chimpanzees it is larger than that of any female chimpanzee, and in structure it differs in numerous details from the anthropoid brain.

Casts were shown of the new mandible of the Swartkrans Ape-man *Paranthropus crassidens*, and of some teeth associated with it. The upper incisors ,and canine are almost typically human in structure and as the canine has been abraded by the 2nd incisor there can have been no diastema between them as in *Pithecanthropus robustus*. A cast was also shown of the palate of the female *P. crassidens*.

A Series of Pure Cultures of Algae

By Dr. R. W. Butcher and Dr. N. Reynolds.

(*a*) *Cultivating algae on glass slips*, by R. W. Butcher.

Whilst culture in a liquid medium or on agar is very satisfactory for large numbers of algae and flagellates much additional information has been obtained of the morphology of various sessile and epiphytic algae by placing glass cover slips in a liquid medium. These may be withdrawn at any time, examined, transferred to other cultures or made into permanent preparations. They may also be broken so that a minute fragment containing a single plant can be transferred and in this way uni-algal cultures can be obtained. Demonstrations showed various forms of *Stigeoclonium*, *Ulvella* and *Ulothrix*.

(*b*) *Some cultures of marine flagellates and other minute algae,* by R. W. BUTCHER.

A series of minute flagellates, many of which are undescribed, has been isolated from the sea at the Ministry of Agriculture's Shell-fish Research Station. Among the more interesting forms are a very minute species of *Cromulina,* a markedly metabolic Chrysomonad of the group Ochromandinae and several new Cryptomonads.

The method used in demonstrating the flagellae of these organisms is to place a drop of 2 per cent. Osmic acid on the slide to fix the organisms and to follow this with a drop of a new methylene blue kindly supplied by Messrs I.C.I.

(*c*) The effect of varying the cultural conditions on the form of *Stigeoclonium,* by N. REYNOLDS.

The form of the plant varies with the composition of the culture solution and also with the cultural conditions. Slides were shown bearing plants of the same clone grown in different natural waters, and also grown in the laboratory in culture solutions of different compositions, to show the range of forms from an almost completely prostrate plant to one with a small sole and long unbranched erect filaments.

(*d*) *Artificially induced zoospore production,* by N. REYNOLDS and R. W. BUTCHER.

In *Stigeoclonium* profuse formation of zoospores may be induced by transferring the plants to ' zoospore inducing solution '. This is rich in nitrate and especially rich in phosphate. Spore formation occurs two days after transferring to the new medium. Material of other species (e.g. *Chaetopeltis orbicularis, Ulothrix,* etc.) is also shown.

Twin sporogonia in Polytrichum juniperinum

By G. J. CUNNELL.

A single gametophyte bearing two sporogonia, apparently with a common calyptra, gathered on Littleworth Common, Surrey, in late April 1949, was shown.

Water colour drawings of Cryptogams

By Miss H. D. GARSIDE.

The species of mosses depicted were *Fissidens bryoides* and *Pleuridium subulatum,* and showed enlargement of the whole plant as well as of the capsule, spores, etc. A painting of the hepatic *Lophocolea heterophylla,* with enlargements, was also shown.

The multiform species Jassa falcata (Montagu, 1808)—Crustacea, Amphipoda

By Dr. I. GORDON, F.L.S., for Mrs. E. W. SEXTON, F.L.S.

Jassa falcata (Montagu), one of the ' nest ' building Amphipods has almost a world-wide distribution. It has the added distinction of having caused more trouble to the systematist than any other Amphipod species. This is partly due to the fact that these animals reach sexual maturity long before they attain the maximum size for the species. The diversity of form exhibited by the growth stages of the male is such that they have been referred during the past 140 years to 13 different genera and some 30 different species.

A special study was made of material collected at Plymouth over a period of years, supplemented by breeding experiments. There are two main lines o development leading to the Major Broad and the Major Narrow forms respectively. The differences between these are most marked in the second antenna and the hand of the second gnathopod of the male ; they are less obvious in the females where they are confined to the second antenna. In addition, many Minor Forms termed Intermediates are met with—smaller male forms which, while showing the characters of one or other of the Major Forms, differ from them in the shape of the hand of gnathopod 2, especially in the reduction of the thumb. They do not seem to merge into the Major Forms and it is these that have caused most of the trouble to systematists. Male Intersexes have been met with for the first time. Breeding experiments show that these all belong to one and the same species.

An efficient device for reading microfilms

By F. C. Grigg.

A number of objections arise with the various pieces of apparatus designed for viewing or projecting microfilms, connected with the manipulation of the film and the resolution obtained by the optical set-up. With the former there is the ever-present danger of scratching on the metal guides and sprockets ; also, if the frames are printed in mixed series, transversely and longitudinally, with a fixed viewer this presents a grave disadvantage ; further, it is not usually possible to vary the magnification as one would wish. Direct optical observation is best with illumination behind the film.

A slightly inclined viewing box was used with a ground glass stage. Over it was mounted a Greenough binocular microscope which, by alteration of one pair of objectives, screwing in either way, and two pairs of eyepieces, magnification was obtained with good resolution of 4, 8, 16 and 32 times. These magnifications were adjudged by all as adequate.

The film holder, held closed with a metal clip, is a stout cardboard folder, $8 \times 3\frac{1}{2}$ inches, covered with leather cloth and having a central rectangular aperture. Inside is another folder lined with velvet the same width as the film. The film can be taken out and inserted at any point, can be slid along as desired, and the holder with the enclosed film may be turned around on the stage if a frame printed the other way is encountered. No stage clips are required, the holder may be held or moved quite conveniently with the hands or will lie where placed. Reading is extremely easy even for persons not used to observation with the microscope and the examination of fine detail in photographed specimens avoids the necessity of handling the actual specimens.

Extra-nuclear Cytology—Results of recent researches

By F. C. Grigg.

In recent years more attention has been paid than hitherto to the extra-nuclear components of the cell, and much profit may be gained by a study of living plant cells under a properly set up and efficient system of dark ground illumination. With fixed material improvements are to be found by replacing alcohol for dehydration by dioxan, the use of low melting-point wax combinations for infiltration and more suitable gradation of fixative accordingly.

The exhibits were :—Living scale skin of onion under high power dark-ground illumination showing streaming movements in the cytoplasm. Embryo-sac mother-cell of *Lilium Henryii*, Telophase-I, prepared by a new technique* revealing structural changes in the cytoplasm and transference of nucleic acid globules from the chromosomes to the cytoplasm. Series of photomicrographs exhibiting the Embryosac Cycle from Synapsis to Interphase-I. Lantern slides of these and others showing the internal structure of chromosomes in pollen mother cells.

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* Full details of this method are to be published shortly in the *Journal of the Royal Microscopical Society.*

The use of thin sections of entire organs in morbid anatomical studies

By Professor J. GOUGH and Mr. J. E. WENTWORTH, Department of Patholgy and Bacteriology, Welsh National School of Medicine, Cardiff.

Our original aim in designing this technique was to obtain representative sections of the entire lung for comparison with radiographs taken during life in an investigation of respiratory disease in coalworkers. The method is also applicable to other diseases and to organs other than the lung.

The organs are fixed in 10 per cent. formalin solution, containing 4 per cent. sodium acetate. In the case of the lung the fixative is run into the bronchi from a reservoir to obtain expansion. After fixation for at least three days and preferably much longer, an inch thick slice is washed for three days to remove the formalin. It is then placed successively for three days in each of 10 per cent., 20 per cent., and 25 per cent. gelatin solutions in an oven at 35°–37° C. Each of these solutions contains either 2 per cent. Phenoxetol or 1 per cent. Propylene Phenoxetol as an antiseptic and as a preservative of colour.

A block is made of the slice embedded in the 25 per cent. gelatin by casting in a rectangular perspex mould with a loose bottom. The block is hardened by immersing for a week in the formalin solution. It is then fixed to the block holder of a special microtome by means of gelatin solution.

Sections are cut at about 500μ. They can be mounted on paper by flooding a sheet of perspex with a warm solution containing gelatin 7·5 gms. per cent., glycerin 7 ml. per cent. and 10 ml. per cent. of 10 per cent. camphor in methylated spirits. The section is laid in the solution and covered with a sheet of filter paper. After lightly squeegeeing to remove air bubbles and surplus solution, the paper is allowed to dry thoroughly, first in air and then at 37° C. The paper then may be stripped off with the section attached. This makes a permanent preparation in natural colour. The sections may also be mounted in thin perspex cases in the usual mounting fluids.

Enzymatic Maceration of Skeletons

By Mr. P. G. LUTHER, Department of Eugenics, Biometry and Genetics, University College, London.

The methods usually used for the preparation of skeletons cannot easily be adapted for large-scale work. Genetical studies on the variations of the skeleton of the house mouse carried out in this laboratory required a method by which large numbers of skeletons could be prepared rapidly. This was achieved by digestion of the animal by means of the proteolytic enzyme papain. I have done up to twenty or more mouse skeletons per day, and altogether more than 1,500 specimens have been prepared by this method.

The technique is very simple. The mouse is skinned, eviscerated and boiled for about ten minutes. After cooling down, it is incubated overnight at 37° C. in about 100 cc. of a freshly prepared 1 per cent. solution of powdered papain in saline in a well-stoppered half-pint milk bottle. Next morning the specimen is again boiled for a few minutes in a beaker and subsequently poured into a flat-bottomed glass dish ; care must be taken at this step that no bones are left behind sticking to the walls of the beaker. The turbid supernatant fluid is decanted and replaced by clean water repeatedly until nothing but a clean deposit of isolated bones is left in the glass dish ; the washings are kept until the bones have been gathered and checked for completeness, as it sometimes happens that one of the smaller bones is lifted up by a gas bubble and poured away. The bones are bleached in H_2O_2, defatted in acetone and ultimately dried. The whole process can be carried through in twenty-four hours, though rather more time is sometimes required for thorough defatting. As different batches of papain differ in their activity, the concentration and time of treatment may have to be varied slightly.

The preparations are very clean and completely free of periosteum. As cartilage is digested by papain, the epiphyses of the long bones, etc., become separated from the diaphyses in young animals. Similarly, the skull, even of adult mice, is largely disarticulated ; quite small bones, such as the auditory ossicles, can be recovered perfectly clean and intact. The method has also been used successfully on rabbits, guinea-pigs, cats, frogs and salamanders. Its only disadvantage is the unpleasant smell developed during incubation and the second boiling of the specimens, which makes it advisable to carry out these operations in a fume cupboard.

Water-colour drawings of Crassula species

By Mrs. VERA HIGGINS.

The exhibit consisted of about fifty water-colour drawings of the S. African species of *Crassula*, the plants having been grown and flowered in England.

The study of succulent plants is complicated by the difficulty of preparing satisfactory herbarium specimens ; it was therefore thought that a review of the genus *Crassula* from living material would be useful. This method is a slow one since it takes time to establish a growing plant and to bring it to the flowering stage. There is also the difficulty of keeping it true to type in cultivation, but experience of growing succulent plants in England, especially those from S. Africa, suggests that it is not impossible, since the conditions in a greenhouse are under control.

Besides plants which have been growing in this country for a number of years, fresh material is being sent from S. Africa (by Air Mail); its condition on arrival is noted and another record made of the plant when it has reached maturity. Cuttings and rooted plants only are being used. The amount of hybridization that occurs in nature is uncertain ; in a greenhouse hybridization is not uncommon, therefore it is not proposed to include plants raised from seed.

This method is intended to supplement not to supplant herbarium material, but knowledge of a plant's behaviour throughout the annual life cycle should have considerable taxonomic value. Many of the early illustrations of Crassulas, those of Jacquin and de Candolle for example, were made from plants which had been grown in Europe, and that the treatment given them was too hot and too moist is evident from the forms of the plants in the drawings. A knowledge of behaviour under cultivation may help to elucidate some of the problems.

The work is only in its initial stages ; it is proposed to collect as much material as possible before any critical revision is undertaken.

Insect Visitors to fruit blossoms

By Mr. C. H. HOOPER.

Mr. C. H. Hooper exhibited a collection of insects which he had made from the flowers of almond, peach, cherry, plum and blackberry, between the months of March and August. The collection included 44 species of Hymenoptera, 35 of Diptera, 18 of Coleoptera and 8 of Lepidoptera (7 butterflies and 1 moth).

Drawings of Antelopes, etc., by Waterhouse Hawkins

By Dr. A. Tindell Hopwood, Sec.L.S.

Studies of antelopes, probably drawn when preparing the plates for the volume describing the 'Hoofed Quadrupeds' in Lord Derby's menagerie at Knowsley Hall.

(1) Mammalian clines associated with the rules of Bergmann, Allen and Gloger. (2) A sub-species chain in Peromyscus maniculatus where the end forms overlap and do not interbreed. (3) Two closely related species which overlap in their range but do not interbreed—Apodemus sylvaticus and A. flavicollis

By Miss E. M. O. Laurie.

Exhibits were shown illustrating the geographical rules of :—

(*a*) Bergmann : In nearly related animals, the smaller species lives in the warmer parts of the range and the larger in the colder. Exhibits : Californian hare (*Lepus californicus*), from the warmer parts and Arctic hare (*Lepus arcticus*) from the colder parts of the range.

(*b*) Allen : Protruding body parts, such as tails, ears, feet and bills tend to be shorter in colder climates, when closely allied forms are compared. Exhibits : Californian hare (*Lepus californicus*) and Arctic hare (*Lepus arcticus*) as above; the Bat-eared fox (*Otocyon megalotis*), from a warm climate, has large ears and tail compared with those of the Arctic fox (*Alopex lagopus*) from a cold climate.

(*c*) Gloger : An increase in the warmth and humidity of the habitat tends to be correlated with increase in the melanins, i.e. the animals are darker in the warm damp parts of the range. Exhibits : Striped-mice (*Lemniscomys dunni, L. lynesi* and *Rhabdomys pumilio*) showing light forms from the cooler, drier part of the range and dark from the warmer damper part, and the squirrel (*Heliosciurus gambianus*) which shows similar correlations.

Clines. The term cline was introduced by J. S. Huxley, in 1938, to denote a gradation in the measurable characters of an animal such as size, proportions and pigmentation which tend to be correlated with climatic and geographic conditions (Bergmann's, Allen's and Gloger's rules) and show parallel gradations. Exhibit : An example of a mammalian cline is the gradation of coat-colour of the deer-mouse (*Peromyscus polionotus*) which is related to changes in the colour of the soil.

Species formation by geographical variation. Exhibit : An excellent demonstration of species formation by geographical variation is provided by sub-species chains in which the end forms overlap in distribution but do not interbreed and would be considered good species were it not for the intergrading forms. This is shown by the overlapping circle of races in the deer-mouse (*Peromyscus maniculatus*) in Glacier National Park, Montana, U.S.A.

Two closely related species may overlap in their range but not interbreed. Exhibit : Two species of the long-tailed field mouse (*Apodemus sylvaticus* and *A. flavicollis*) in Great Britain.

Peripatus : gaits and footprints

By Dr. S. M. Manton, F.R.S.

[A full account will be contained in a paper to be published in the *Journal, Zoology*.]

Variation in Purpura lapillus Linn.

By Dr. W. J. Rees.

The shell of *Purpura* occurs in two distinct forms ; the smooth variety commonly found on the shore and the variety with an imbricate shell on submerged reefs below water mark.

Lamarck regarded the latter as a distinct species, which he called *imbricata*, but it is now known to be nothing more than an ecotype. In its most marked form it is a delicate shell which could not possibly survive undamaged if it were subjected to much wave action.

Purpura shells are found in a number of colours from white to yellow, brown and purple. It has been demonstrated (Moore, 1936, *J. mar. biol. Assoc.*, **21,** pp. 61–89) that colour is correlated with diet, which varies from one of mussels (*Mytilus edulis*) to one of barnacles. Brown and mauve colour varieties are unquestionably dependent on the abundance of *Mytilus* in the diet. Experimental feeding of animals with shells of these colours on *Balanus* only resulted in a disappearance of the colour and the laying down of a white addition to the shell margin. Pigment was laid down once more in the shell margin when the diet changed back to *Mytilus*. Yellow shells occur in specimens feeding on a *Mytilus*-free diet.

Some remarkable handwritings in the Society's collections

By S. Savage.

Examples were shown from the Linnaean and Smithian correspondences, and the reasons for the selections stated. They included a letter from Dodoens to Clusius ; one from G. Prevost, peintre du Roi au Palais de Trianon ; one from L. Gérard to Sir James E Smith ; and an example of minute handwriting sent by H. J. Noordgren from Batavia.

(1) An aquatic discomycete resembling Ombrophila Clavus (A. & S.) Phil. (2) A case of syncotyly in the common radish, Raphanus sativus Linn.

By Dr. J. K. Spearing.

(1) An aquatic discomycete resembling *Ombrophila Clavus* (A. & S.) Phil.

The specimens shown were collected from a very shallow ' aquarium ' at St. Mary Cray, Kent. They resemble *O. Clavus* var. *pallens* in some respects, whereas in other features they stand closer to the genus *Helotium*. They may possibly belong to Mr. F. Currey's species, *H. aquaticum*, described in *Trans. Linn. Soc. Lond.* **24**, p. 154 (1863), and apparently not found since. A full description will be published elsewhere.

(2) A case of syncotyly in the common radish, *Raphanus sativus* Linn.

The seedling exhibited was found growing in a bed of radishes in the exhibitor's garden. It was preserved in spirit, stained *in toto* and mounted on a microscope slide in Canada balsam.

The two cotyledons are completely united unilaterally in the petiolar region to form a sheath-like structure apparently open throughout its length on one side. The two laminae are almost completely coalescent, but show distinctly the two emarginate apices and the midribs. The fused cotyledons stand terminally on the hypocotyl, and the plumule is emerging laterally.

Cases of syncotyly, although not exceedingly rare, are of theoretical interest in illustrating one way in which a monocotyledonous condition could arise. Such a case has previously been reported in *R. Raphanistrum*, as well as in several other species belonging to various families, but it is believed not previously in *R. sativus*.

PROCEEDINGS OF THE GENERAL MEETING ON 12 May 1949

Dr. W. E. Swinton, Vice-President,
in the Chair.

The Proceedings of the General Meeting held on Thursday, 28 April 1949, having been circulated, were taken as read and confirmed.

The following were thanked for gifts made to the Library since the last Meeting :—Madame M. Hager-Davall, Professor Jan Kořinek, the Rev. Emile Licent, S.J., Mr. C. A. W. Sandeman, Professor F. E. Weiss, F.R.S., and the East African Agriculture and Forestry Research Organization, Amani.

The following Fellow signed the Obligation in the Roll and Charter Book, and was admitted a Fellow :—Mr. Frederick Clifford Fryer.

Read for the second time, certificates of recommendation for election to Fellowship in favour of Professor Arthur Roy Clapham, M.A., Ph.D., and Leslie Francis Seawell Ward, M.A.

Read for the second time, a certificate of recommendation for election to Foreign Membership, in favour of Dr. David Fairchild, of Coconut Grove, Florida, U.S.A.

Candidates for membership were balloted for and elected :—

Fellowship.—Nazir Ahmad, M.Sc., Ph.D., Professor Leslie John Audus, M.A., Ph.D., Guy Oldfield Allen, M.A., Frederick James Fitzmaurice Barrington, F.R.C.S., Robert Churchill Blackie, M.Sc., Ph.D., Professor James Dixon Boyd, M.A., M.D., B.Ch., M.Sc., Professor Francis William Rogers Brambell, B.A., D.Sc., F.R.S., Douglas Maxwell Bryce, B.Pharm., Hira Lal Chakravarty, D.Sc., Lionel Percy Clarke, M.R.C.S.(Eng.), L.R.C.P.(Lond.), Peter Hadland Davis, Frederick Claude Deighton, O.B.E., M.A., Miss Constance Margaret Eardley, M.Sc., Dr. Ronald Darnley Gibbs, Miss Maud B. E. Godward, M.Sc., Ph.D., Edward Cowper Green B.A., Peter S. Green, B.Sc., Brian J. Grieve, M.Sc., Ph.D., Ronald Herbert Hall, Mrs. E. Amy Hodgson, Edward Charles Talleyrand Holsinger, B.Sc., Charles Adrian Hopkins, B.Sc., Professor Cornelius Jan van der Horst, D.Sc., Miss Frances Ethel Ince, M.Sc., D. M. A. Jayaweera, B.Sc., Miss Eleanor Mary Ord Laurie, M.Sc., Rev. Peter E. Lye, O.S.B., B.Sc., Mrs. Una Christina Mason, M.Sc., Professor Peter Brian Medawar, M.A., D.Sc., F.R.S., Mannath Devidas Menon, M.A., B.Sc., Oliphant Bell Miller, The Earl of Morton, M.A., Miss Betty Louise Moss, M.Sc., Ph.D., James Hartley Murgatroyd, Miss Margaret Naylor, M.Sc., Hubert Decimus Noronha, M.A., M.Sc., Ph.D., Mrs. Mary Peach, B.Sc., William Victor David Peiris, M.A., B.Sc., Leonard William Poel, B.Sc., Oleg Vladimir Polunin, M.A., Ronald Purdy, B.Sc., Rev. Professor W. Rees-Wright, M.Sc., Ph.D., Surendra Rohatgi, B.Sc., Leo Sachs, B.Sc., Redcliffe Nathan Salaman, J.P., M.A., M.D., F.R.S., Christopher Albert Walter Sandeman, Mrs. Cecil Ivry Sandwith, Edmund A. C. L. E. Schelpe, George Reginald Allen Short, Ph.C., Norman Willison Simmonds, M.A., Mahendra Raj Suxena, M.S., Geoffrey Brian Boyd Thomas, B.Sc., Miss Elisabeth Anna Ullmann, B.Sc., Miss Joyce Winifred Vickery, M.Sc., Miss Lille Ethel Wagge, B.Sc., Ph.D., Ernest Alfred Walters, Alan Douglas Whitehead, B.Sc., John Frederick Woolman, and Robert Wright, B.Sc.

Foreign Membership.—Professor Dr. Otto Jaag.

Associateship honoris causa.—Dr. Robert Lloyd Praeger and Dr. Arvid Hjalmar Uggla, R.N.O., R.V.O.

The following communications were read and discussed :—

Mr. I. H. Burkill. An interruption in the after-ripening of *Tamus* which alters the range of temperature controlling germination. (Discussed by Sir Nigel G. Ball, Bt., Dr. B. Barnes, Mr. F. C. Grigg and Dr. Leon Hayward.)

Dr. A. Tindell Hopwood, Sec.L.S. The influence of physical theory on biological thought. (Discussed by Prof. A. J. E. Cave.)

The following papers were read in title :—

'Contributions towards the fungus flora of Uganda.—IX. The Uredinales of Uganda.' By E. M. Wakefield, M.A., and C. G. Hansford, M.A. [Printed in full, see p. 162.]

'Goethe's interest in British botany.' By John Hennig, Ph.D. [Printed in full, see p. 199.]

'Studies on the Onychophora.—VIII. On the locomotion of *Peripatopsis*.' By S. M. Manton (Mrs. J. P. Harding), Sc.D., F.R.S. [To be printed in the *Journal, Zoology*.]

AN INTERRUPTION IN THE AFTER-RIPENING OF TAMUS WHICH ALTERS THE RANGE OF TEMPERATURE CONTROLLING GERMINATION

By I. H. Burkill.

(With a text-figure.)

When the berry of *Tamus communis* L. is ripe, the seed is not, but is in need of six months and more of moist conditions to complete an after-ripening. Temperatures for this after-ripening have a range that is liberal enough to allow it to proceed in the English summer and in the English winter ; but when the after-ripening has been completed, as judged by the ability of the seed to respond, a conjunction of three factors—(i) its own readiness, (ii) moisture as in the after-ripening, and (iii) a certain precision in temperatures—is necessary to enable the energy so far expended in development to break out into the many-sided growth of germination. Seeds at any phase in the after-ripening become dormant if without water ; and the English summer dries them in the soil to this condition —a condition which it is convenient to call drought-dormancy. It is natural to believe that unsuitable temperatures, even when the range is liberal, induce at times a temperature-dormancy and that when after-ripening has been completed there is probably a period of temperature-dormancy holding germination back until the right temperatures arrive. These temperature-dormancies are one and the same, save that there develops a narrow sensitivity.

The drought-dormancies of the English summer, added to the obligatory months of after-ripening and to whatever period of temperature-dormancy there be imposed by waiting for right temperatures, commonly stretch the interval between the ripening of the berry and the act of germination to more than a twelve-month, during which there is a mortality of the seed so great that the geographic range of the species must be largely, and in some sectors entirely, determined by it.

A seed needs to obtain burial for success. It has a mechanism for this. Having fallen to the soil and come to rest in a crack, it expands if wetted and thereby enlarges its bed ; then it contracts on drying and sinks a little ; by this means it works its way downwards so as to pass beyond the reach of frost which kills seedlings at germination if it reaches them, and also to find a depth where the soil-cover considerably equalizes the moisture. Intermittent moisture is the agent, but continuous moisture is aimed at, so that there is a conflict within the plant's needs. It was this which induced me to plan experiments seeking to ascertain if the demand for water alters during after-ripening, as the demand in temperature seems to alter. The length of the after-ripening makes *Tamus* most convenient for such experiments. As burial is a first need, an ideal climate for *Tamus* would seem to be one where a rainy season is introduced by a considerable period of well-spaced showers.

My experiments disclosed a character that has considerably interested me, namely that the rough-handling of withdrawing water, which I shall call shock, if done in the first part of the after-ripening when burial should be in an early stage, catches the seed in a phase of sensitivity that is part of the development of the temperature-responsiveness.

For my experiments I collected in the beginning of October 1947, a large supply of berries from hedgerows near Paignton, Devon ; washed the seeds and allowed them to become air-dry. By the 15th of the month I had enough. Then, using a thimble, I put samples of about 320 seeds into small linen bags, each tagged with instructions for treatment ; some were to be robbed of water for one month, some for two months and some for three months ; some from the beginning of the experiment, some from the beginning of the second month and so on ; two were set aside as controls, never to be without water ; one sample was set apart to be wet or dry in alternate weeks ; another in alternate fortnights and a third to be dry for one week at the end of each calendar month.

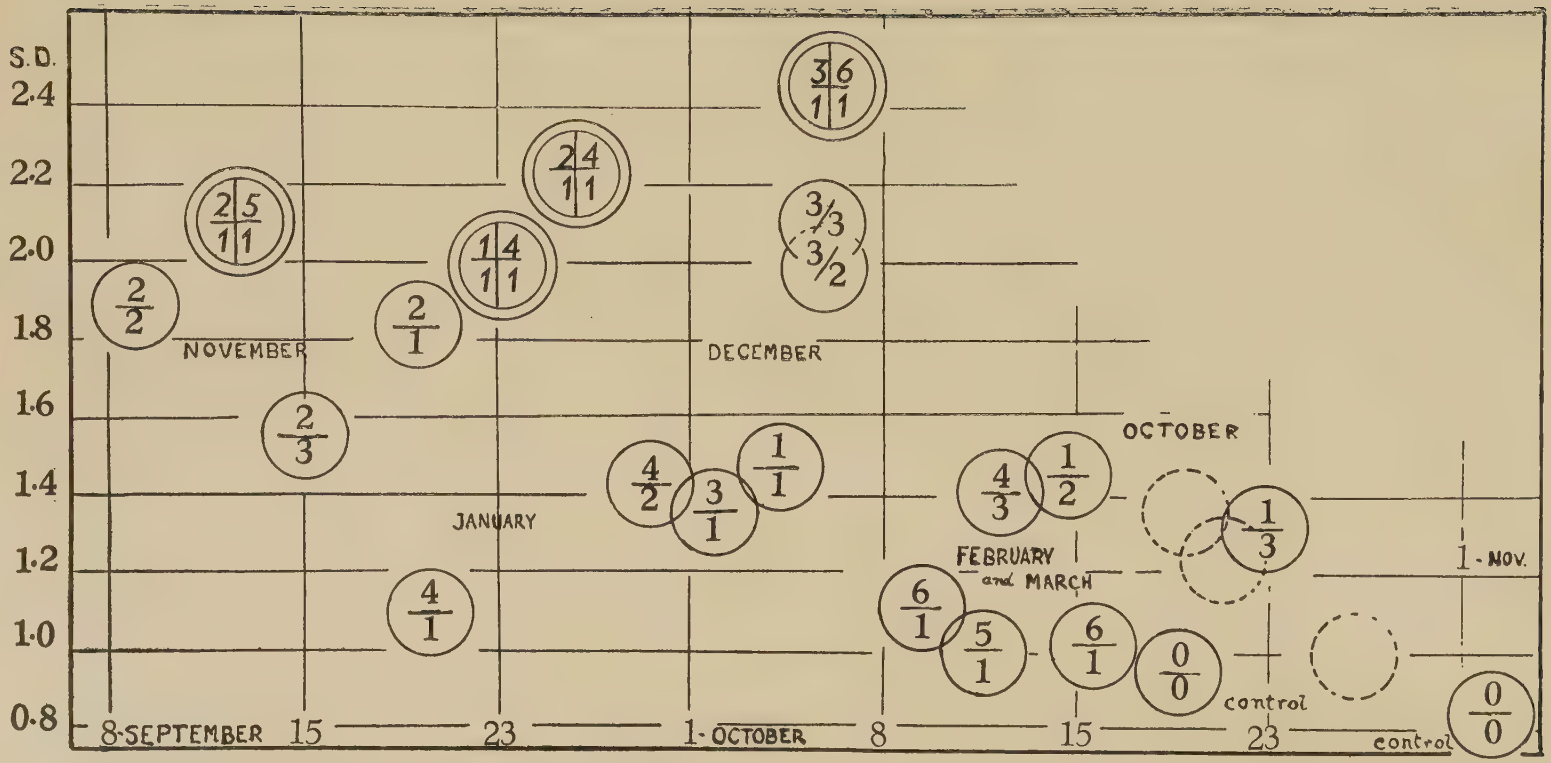
It suffices to cause a seed to touch a wet surface for it to take up water ; and water was throughout given in this way. The linen bags served until 15 April, i.e. for the obligatory months of after-ripening ; after that small saucers were substituted so that inspection might be easy. Light was excluded ; and the experiment was done within my house with frost excluded, but without artificial heat. When on 15 April the linen bags were discarded, about fifty seeds were withdrawn from each sample, dried and kept air-dry, i.e. dormant, for the next five months ; but all the rest received continuous moisture in a way that equalized their opportunities for germination. The reason for withdrawing seed is given in the second paragraph below. It soon became evident that the shock of drying had been extensively lethal ; and that the duration of the dryness had had much less effect. The extent of the killing could not be measured directly, but could be estimated from the numbers that survived to germinate.

There were no germinations prior to the removal of the samples to saucers ; the first was on 30 April and was followed by another four days later. Then there was a break of rather more than two months. The two isolated germinations will be disregarded. The genuine returns began to come in at the end of the second week of July and germinations followed in an unbroken succession to the end of November. Summing in periods of half-months those of the month-to-month experiments, they were :—

July		August		September		October		November	
2	48	11	99	173	265	346	416	208	54

June and July 1948, were phenomenally cold ; apart from this the season does not need comment ; and it is obvious that germination occurred at an unexpectedly wide range of temperature. It was seeds which had received the shock of being made dry which germinated at all the earlier dates.

I am now able to explain the purpose of withdrawing seeds from each sample on 15 April. It was foreseen that when germination ceased the question would



Each circle represents a sample of about 270 seeds. The upper numeral in the circle is the month of withdrawal of water, the lower the duration of the withholding. Each circle shows by horizontal position the measure (abscissae) in which the germination of the seeds was advanced; and by vertical position the inaccuracy (ordinates) of the temperature response, measured by the Standard Deviation.

arise—had all the seeds which had come to the phase of readiness-to-germinate germinated, or had the season arrested germinations. So the seeds that had been withdrawn on 15 April were given water again on 15 September, by which time they presumedly had lost five months that the others had had in preparation for germination. From 15 September they had all the water necessary and they commenced to germinate at the beginning of December, continuing to do so into January, whereby they proved that season was not causing the cessation of germinations in the rest.

As soon as I had satisfied myself of this, I made for all the samples curves of error on the dates of the germinations, found the date of the mode and calculated the Standard Deviation, i.e. the departure from simultaneousness of germination. In the diagram (p. 153) each circle represents a sample ; abscissae are by dates ; ordinates are by deviations from simultaneousness, and each circle is placed where the date of its mode and the amount of its deviation intersect so that it tells by its position how early and how irregular was the germination in the sample which it represents. The numerals within the circles give the treatment, the upper of them the month of shock, the lower the duration of dryness ; thus, 1 over 1 means that the shock was on the first 15th and the dryness lasted for one month ; 1 over 2 means that the dryness lasted two months ; 0 over 0 means that there was no shock, the two circles so marked being those of the controls. Doubled circles are the circles of samples that received two shocks, and dotted circles of samples which were not on the month-to-month list.

The reader will observe the position of the controls to be at the right hand lower corner of the diagram, showing that the controls did not germinate until late, nor was their approach to simultaneousness altered ; they had had not merely six months under moist conditions, but an additional six months, without damage to their efficiency. As against them it is apparent that the interruptions in the water-supply suffered by the others brought about various degrees of departure from normal. Summed by the number of months of moisture that all the seeds in the month-to-month experiments had had :—after six months there were 17 germinations ; after seven 97 ; after eight 257 ; after nine 377 ; after ten 331 ; after eleven 178 ; after twelve 72 ; and after thirteen 13 ; which is as if nine were optimal ; but this appearance is only the consequence of the lay-out of the experiments.

The greatest interest in the diagram is that shock in November advanced the mean date of germination more than shock in any other month ; that December came next ; and that shock in February and March scarcely advanced it. This result does not square with the lethal effects of the shock which were greatest for the month of March and fell in this order :—March, October, February, November, December, January, the average number of germinations per sample, having been

after shock in

October	November	December	January	February	March
43	73	88	91	54	29

Can it be that in England there is a mid-winter approach to dormancy which protects from death ? Whether this be so, or not, a month earlier than mid-winter a condition apparently exists in the developing embryo wherein the development of the relationship between germination and temperature can be prejudiced several months ahead, as the onset of summer development in winter cereals can be prejudiced by chilling at the commencement of germination in the agricultural device of Vernalization. Both get on faster so to speak by not observing the traffic lights. *Tamus* seed, in consequence of the impairing of this temperature-germination relationship, germinates, when set to do so, against falling temperatures, as was the case in my experiments, before the normal stimulation is reached. I use the word impair because it is impossible to regard a shock which is lethal at its worst, to be anything short of injurious when failing to be lethal; I look at it as knocking out a control which must have been a climatic adaptation epigenetically. One would not expect the plant to be a gainer by the knocking out, though under a considerable and unlikely transfer of the seed to a new climate it could increase the chance of germination, by freeing the germination from a control no longer useful.

The diagram shows that two shocks in succession greatly disturbed the Deviation; my other data show that the lethal effect of the two approximated to the intensity of whichever of the two was most severe when given alone; thus, shocks in October and January left 50 seeds to germinate which figure is near the '43' in the statement above; shocks in November and January left 74 seeds to germinate which figure is virtually the '73' of that statement; shocks in November and February left 41 which is near the '54' for February; and shocks in December and March left 18 which may be compared with the '29 standing for March in the statement.

I am unable to explain the dispersal of the dates of germination after a single shock in October and after a single shock in January; and to explain them I plan further experiments.

Interruptions of moisture of short duration (see the dotted circles in the diagram) caused no marked advancement of the date of germination and very little increase of Deviation. The lowest of the three dotted circles is that for the sample wet or dry week by week; the next that of the sample wet or dry fortnight by fortnight; and the uppermost is that of the sample dried for a week at the end of each month. The reader will observe that all the dotted circles are close to the controls in a measure which suggests that short breaks in the moisture are not injurious. It is as if the seed-coats take the rub and fend the embryo from drying for enough time for that to be the case.

I have shown (*Journ. Bot.* **48,** 1939, p. 48, curve D of the diagram there) that Deviation is increased by ageing of the seed. Shocks as I gave them may be regarded as hastening ageing.

THE INFLUENCE OF PHYSICAL THEORY ON BIOLOGICAL THOUGHT

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In one form or another, the phrase 'physics is the fundamental science' is met with in the works of writers of widely differing calibre. It was in the mind of one of the greatest thinkers of this century when he wrote, 'Every special science has to assume results from other sciences. For example, biology presupposes physics. It will usually be the case that these loans from one specialism to another really belong to the state of science thirty or forty years earlier. The presuppositions of the physics of my boyhood are to-day powerful influences in the mentality of physiologists. Indeed we do not need to bring in the physiologists. The presuppositions of yesterday's physics remain in the minds of physicists, although their explicit doctrines taken in detail deny them.' (Whitehead, 1938, p. 178.)

By Science is meant the study of Nature, or Natural Science, that is to say, the study of the observable or sensible universe. It is a factual science; it presupposes the existence of facts fulfilling the essential condition that they shall be observable. A fact that cannot be observed is not a scientific fact; since Science cannot observe it she is unable either to affirm or to deny its existence, neither is she able to formulate a judgement concerning it. In this way Science selects from the totality of facts only those portions which are fitted to serve the ends she has in view, with the direct consequence that she is precluded from a study of the thing in itself, and is restricted to studying its behaviour. To quote Whitehead again, ' The physical things are each to be conceived as modifications of conditions within space-time, extending throughout its whole range. There is a focal region, which in common speech is where the thing is. But its influence streams away from it with finite velocity throughout the utmost recesses of space and time . . . For physics the thing itself is what it does and what it does is this divergent stream of influence.' (1933, ch. IX, § vii.)

The claim is not that physics describes the thing in itself, but that it describes how the thing behaves. This is also true of biology. When a geneticist speaks of certain phenomena in terms of genes, he does not explain why the phenomena occur, but describes what happens when they do occur. He relates two phenomena, each to the other, and states a probability that when one of them is observed, the other also will be observed. In this way he provides an analysis of certain aspects of the behaviour of the organism.

There is here a parallel between physics and biology which was hidden from the Greeks. We regard physics and biology as separate sciences, but to the Greeks biology was a branch of physics, and an unimportant branch at that. Moreover, their picture of the visible universe was very different from ours. Plato said of philosophy that, ' the subject does not admit as the sciences in general do, of exposition ' (Taylor, 1948, p. 23, footnote) ; even so, on the one occasion when he did write on scientific matters, in the *Timaeus*, he still refrained from formulating a system, probably because ' that which is apprehensible by thought with a rational account [i.e. mathematics and dialectic] is that which is unchangeably real ; whereas that which is the object of belief together with unreasoning sensation [i.e. the visible universe] is the thing that becomes and passes away, but never has real being.' (*Timaeus*, 28). From this he draws the conclusion that there can be no exact science of the visible world of nature because it is always changing, ' consequently it is fitting that we should in these matters accept the likely story and look for nothing further.' (*Timaeus*, 29 D) The authorities differ widely in their interpretations of the *Timaeus*, but there is general agreement that Plato's views were mechanistic, and that he regarded change as a function of geometrical structure.

Plato's colleague, and erstwhile pupil, Aristotle, was no mathematician, but he was the foremost zoologist of antiquity, and a great professional expositor. His strong biological bias is to be traced in all his writings, no matter what their subject, and the exigencies of teaching led him to attempt to reduce everything, even the animal kingdom, to systematic order. In the course of his work he defined many things ; among them was the physicist, ' he who concerns himself with all the properties active and passive of bodies or materials thus or thus defined ; attributes not considered as being of this character he leaves to others, in certain cases it may be to a specialist, e.g., a carpenter or a physician, in others (*a*) where they are inseparable in fact, but are separable from any particular kind of body by an effort of abstraction, to the mathematician, (*b*) where they are separable both in fact and in thought from body altogether, to the First Philosopher or metaphysician.' (*De Anima*, 403*b*.)

From this definition two conclusions are to be drawn, first, that Greek physics covered the whole field of nature, and, second, that mathematics was an abstraction from it. To-day the scope of physics is considerably narrower, but Greek cosmology made a universal physics inevitable.

In the Greek view, nature was a material something extended through space, a something, moreover, which, because it moved and its motion arose from within, was alive and possessed *psyche* or soul, and which, because its motion was orderly, was also intelligent, possessing mind. This much was common to Plato and Aristotle, but, whereas Plato's theory of change implied the existence of an external cause, Aristotle explained change as the result of a nisus, or urge, arising from within. Such a theory, which allows of gradual change in a definite direction, might be regarded as containing the germ of a theory of evolution, but Aristotle was quite certain that there was no connection between changes on the earth and possible changes elsewhere. ‘ It is absurd ’, he wrote, ‘ to make the universe to be in process of change because of small and trifling changes on earth, when the bulk and size of the earth are surely as nothing in comparison with the whole universe.’ (*Meteorologica*, 352*a*.)

Before and during the Hellenic period, and for many centuries afterwards, space was three-dimensional, and time was a separate entity composed of a succession of instants. Under these conditions, smooth, even motion is not possible. Zeno realised the difficulty when he posed his famous problem of the arrow ; Aristotle tried to overcome it, and pointed out that a given kind of motion requires a given amount of time in which to take place. In this he anticipated the teachings of modern physics, but the difficulty remained ; it is inherent in discrete space and time, and is beyond solution. Thus the physical background of Aristotle's thought put him on the track of an evolutionary doctrine, and at the same time deprived him of the means whereby it might be brought to fruition.

The next important period was from the middle of the seventeenth to the middle of the eighteenth century. It was the period of Newton, Ray, and Linnaeus. Newton had a long line of precursors extending back at least to the middle of the sixteenth century. Galileo died in 1642, the year that Newton was born, and Descartes died eight years later. Ray, on the other hand, had no precursors of any stature after Aristotle and Theophrastus, and the greater part of his work was incontestably his own invention.

Between them, Galileo and Descartes expelled the *psyche* from the universe. This was more especially the work of Descartes, who distinguished sharply between mind and matter. Newton was left to explain the phenomena of a dead world. Nature was no longer alive, intelligent, and extended through space, but composed of a multitude of particles of dead matter scattered in empty space, When the particles moved, their motion was to be ascribed either to the action of gravitational forces, or else to the result of impact. In each case, motion was imposed from without ; it no longer arose from within.

A universe of this type provides no challenge to the idea of fixity of species. The essence of a dead Nature is that it is immutable except for the influence of external agents. When to this are added a three-dimensional space, and a time composed of a succession of instants, the physical background is ideal for the development of systems of classification, because every event is determinate and precisely located in space and time. Consequently one is not surprised to find that the great biologists of the period, first Ray, whom Cuvier called the founder of modern zoology, and, after him, Linnaeus, busied themselves with naming plants and animals, and arranging them in appropriate pigeon-holes.

During the following century, from the tenth edition of the *Systema Naturae* to the publication of the *Origin of Species*, the fundamental physical presuppositions of biology remained unchanged, and the apparent progress in taxonomy was only superficial. It was entirely due to a steady flow of new discoveries, and to ever-growing attention to fine points of detail. Physics and the sanctions of religion were united in making the development of an evolutionary philosophy all but impossible, and when, three-quarters of a century after Newton, an apostle of evolution did arise in the person of Lamarck, he was a free-thinker, whose theory of biological motion largely depended upon the action of external forces.

This was the one type of evolution possible in a Newtonian universe, but it was derided and scorned none the less. Men's minds had become so attuned to the idea of a fixed order of things that the doctrine of catastrophism, of which Cuvier was one of the most distinguished proponents, was the only acceptable explanation of that succession of life which the geologists were beginning to discover in the rocks. Any suggestion of evolutionary progress was anathema, whether it accorded with physical theory or not.

The *Origin of Species* ushered in what may be termed the Darwinian Interlude. For the next half-century the predominating influence over the minds of men was exercised by biology and not by physics. Doubtless the novelty of the theme had much to do with it, but even more weight must be ascribed to the confusion which reigned in the physical sciences, and was reflected in biological thought.

The universe, an improved model of the Newtonian universe, was a gigantic machine, which was slowly running down and would one day cease to function; space, no longer empty but filled with aether, was still three-dimensional, and time still a succession of instants. In other words, time continued to be abstracted from space and matter, just as it had been in the days when Zeno pondered over the arrow in flight. That abstraction, which underlay the physical presuppositions of the current biology, was the cause of the curiously anomalous position of the doctrine of evolution.

Moreover, because it was a machine, the universe could be resolved into the parts of which it was built up, consequently, living organisms came to be regarded as the parts in current use, and the organisms of past ages were taken to represent old-fashioned, less efficient parts, which had fallen out of use and been cast aside. There was then, as there still is, an unexpressed discontinuity at variance with the fashionable evolutionary doctrine of a gradual upward progress from the unicellular state to the majesty of man. (A curious reflection of the mental atmosphere of the time is seen in the fact that no one spoke of the evolution of *Sacculina* or *Lernaea*. Organisms which behaved so disgracefully did not evolve, they degenerated.) Nevertheless, the study of Nature, interesting and inspiring though it might be, was, at bottom, shot through and through with serious contradictions which rendered it completely unintelligible.

Quite apart from the fact that the mere existence of a machine necessarily implies an external maker, and that the scientists were making an unwarrantable excursion into metaphysics in discussing the point as scientists, the machine itself resembled no other machine in that it was self-improving, self-renewing, and, at the same time, slowly running to a standstill as its entropy increased. In addition, the machine was looked upon as a mere aggregate of its parts. This last is a fallacy which still lingers in many quarters, but that it is a fallacy can be shown by two simple examples, one numerical and one chemical.

The equation

$$3+4=7$$

is absolutely true, it expresses the whole truth of the sum of three and four. If the equation is transposed, thus,

$$7=3+4,$$

its truth is only partial, because seven is not only the sum of three and four, but also the sum of any other combination of integers fulfilling the condition that they add up to seven. Again, a molecule of water is far from being an aggregate of two atoms of a gas called hydrogen, and one atom of another gas called oxygen; it is a substance entirely different from either element, and it possesses entirely different properties.

Similarly, a living organism is very much more than the sum of its parts. Text-books divide the body into various systems, the skeleton, the muscles, the nerves, and so on, but in the living body all these so-called systems interact, and the physician must ever remember that signs and symptoms in one system may be indicative of disorder in another.

Many of the difficulties alluded to arose from the separation of life from matter. There was a threefold struggle between physics, chemistry and life. Then, as now, the elementary particle presupposed by physics was devoid of mass, whereas the chemist presupposed a variety of elementary particles each of them possessing its appropriate mass, or ' atomic weight.' Somehow or other the interaction of these incompatibles was manifested as life, but the manner of their interaction was hidden in obscurity.

One consequence of the confusion that reigned in the sciences presupposed by biology was that biology itself was confused. Taxonomy continued to develop on its age-old basis of an analysis of the characters of dead individual organisms, and was unable to progress, except by way of correction and amplification of what had gone before. Evolution, being a continuous process *ex hypothesi*, could not be expressed by orthodox taxonomy, but found separate expression in phylogenetic trees. It was essential to find a place for evolution, although the method of doing so was quite uncertain.

Nevertheless, the many disadvantages issuant from the underlying confusion were not entirely uncompensated. Classical physics possesses the merit that it enables us to think of Nature at an instant. Indeed, to separate time from space is the only way in which this can be done, because Euclidean geometry disappears in the four-dimensional space-time continuum, and does not reappear until we attain to ten dimensions. The manner of its reappearance is complicated, and involves short cuts through the eighth and ninth dimensions ; independent time does not reappear, it is still the fourth dimension. Hence, classical physics and classical taxonomy march forward hand in hand, but an evolutionary biology presupposes an evolutionary physics, and during the Darwinian Interlude that still lay in the future.

Whitehead (1938, pp. 126–7) made some caustic remarks on this period, which he summed up in these words, ' the middle period of the century [was transformed] into an orgy of scientific triumph. Clear-sighted men, of the sort who are so clearly wrong, now proclaimed that the secrets of the physical universe were finally disclosed. If only you ignored everything which refused to come into line, your powers of explanation were unlimited.' And, a few lines later, ' in its last twenty years the century closed with one of the dullest stages of thought since the time of the First Crusade . . . The period was efficient, dull and half-hearted. It celebrated the triumph of the professional man.' Dull it may have been, dead it was not. The dullness was that of a lump of dough set before the fire to rise, but within it the leaven, the idea of evolution, continued to work unseen.

It was the most important half-century since the Renaissance for it prepared the ground for the replacement of a static by a dynamic universe, and for the integration of space and time.

Modern physics may be taken to begin with the recognition of the atom as a compound structure made up of left-handed, negative charges, or electrons, and right-handed, positive charges, or protons. The simplest atom, that of hydrogen, consists of a central proton round which a single electron revolves ; all the others have a nucleus of tightly-compacted protons and electrons with more electrons revolving as satellites in orbits remote from the nucleus. That this ' solar-system ' atom is in some ways out of date is of no great importance, the two significant factors are the replacement of inertia by movement, and of mass by energy. Together with the concept of a space-time continuum, these two new ideas remove the old antagonisms between the physical and biological sciences, as well as the scientific basis of materialism. Instead, they offer a universe which allows of continuous motion in any direction, a universe in which evolution can take place, and in which one would predict that it must take place.

In this modern universe, the word motion becomes ambiguous, for there is not one kind of motion but two. There is the motion which involves not only duration but also a change of position, and there is the motion which involves duration but no change of position. The first type we will call locomotion, and we will restrict the use of motion to the second type. Of these two types, locomotion is the more important as a biological presupposition, because it is the physical expression of change, and so the counterpart of evolution in biology. Motion, on the other hand, is the expression of maintenance. It represents the expenditure of energy in the preservation of identity, whether the identity be that of a physical or of a biological unit.

There is a certain indefiniteness about the behaviour pattern of a particle in locomotion which has long been recognized, but it was not until 1927 that the uncertainty was put into terms of mathematics. The principle involved is this, that the more accurately we determine the velocity of a particle, the less accurately can we determine its position ; and conversely. Heisenberg showed that in both instances complete accuracy is impossible, and that the product of the errors is never less than Planck's constant h. This constant was the starting point of quantum physics, but quantum physics is concerned with quantities so minute ($h=6{\cdot}55\times10^{-27}$ erg-secs.), and is so undeveloped, that it cannot serve as a presupposition in biology. We have to work in the large-scale universe of relativity physics.

The general principle of uncertainty is also applicable to living nature. When an organism is in locomotion, in other words, when it is in process of evolution, one of two courses is open to the biologist ; either he may concentrate on the organism's velocity, which is its evolutionary history, or he may concentrate on its position, which is the stage of evolution it has attained, but he cannot concentrate on both of them at one time.

No matter which course is adopted, the resultant picture will never be sharp in all its outlines. Complete concentration on the velocity is not possible ; if it were, the organism would cease to possess identity. Complete concentration on position is also impossible, because the velocity of an organism in locomotion cannot be ignored altogether. A species, for example, comprises not only the individuals now living, but also an indefinite number of generations which have lived in the past, as well as an indefinite number which will live in the future. These past and future generations are the expression of that part of the velocity which cannot be ignored.

The behaviour pattern of an organism in motion is analogous to, but not the same as, the behaviour pattern of an organism in locomotion. The difference between them is that the former is engaged in maintaining, and the latter in losing, its identity, whereas the analogy arises from the fact that each in its own way is engaged in a process of becoming. A fertilized egg-cell becomes an embryo, and the embryo becomes a larva, or a seedling, which gradually matures, only to pass from maturity to old age, and finally to death and dissolution. Throughout the whole process the organism retains its identity in the narrow sense that John Smith remains John Smith from the cradle to the grave, and it expends energy in the maintenance of that identity. On the other hand, the life-cycle is a continuous uninterrupted process, with no sharp divisions between its different stages. Thus there is an uncertainty attendant on the motion of an organism, precisely as there is an uncertainty attendant on its locomotion. The principle is the same, but it is applied to different entities.

At this stage of the argument it is clear that use of the word organism without qualification involves some ambiguity. The difficulty is largely a matter of definition. It originates in the fact that the phrase ' organism in locomotion ' suggests a species, whereas ' organism in motion ' suggests one of the individuals included within the species. Nevertheless, there is a sense in which the species is in motion, and the individual in locomotion. If it were not for the former, the species could not maintain its identity ; but for the latter, the species could not change its identity. In this sense, the use of organism to cover both the species and the individual does not appear to be a serious error, but confusion may be avoided by employing the terms ' species-organism ' and ' unit-organism ' when the context requires it.

Modern physics provides a finite, four-dimensional universe full of energy expressing itself in patterns of behaviour, and shows that because the patterns depend on movement they are more or less vague and their details uncertain. A certain section of this universe, namely that portion of it which is alive, is studied by the biologist, who finds, as is inevitable, that he, too, is studying patterns of behaviour. The palaeontologist investigates the locomotion of the species-organism, and the neontologist the motion of the unit-organism, but each is obliged to take the work of the other into account in order to complete his own picture. For example, the biochemist, impressed by the relatively uniform composition of the circulatory fluids, has had to enquire into the conditions which obtained in remote geological periods ; conversely, the forms of life in past ages can only be interpreted in terms of the present. The importance of the present in the past increases steadily as the past approaches the present, until, in the Pleistocene, one's knowledge of the present must be equal to, or even exceed, one's knowledge of the past.

Physical theory holds that space implies time because it needs time for development. Time on the other hand implies space, neither can exist without the other, and their development was simultaneous. Pattern is secondary to these primary phenomena ; it must have both time and space in which to develop. Whitehead summed up the consequences of this theory in the famous phrase, ' There is no Nature at an instant.'

Whether they so occur or not, logical priority demands that changes in the presuppositions of one of the special sciences should first affect the basic discipline of that science. Taxonomy is the basic biological discipline, and this essay may be brought to an appropriate close with a brief comment on two modern classifications, one of the Mammalia as a whole, and one of a single group, the Proboscidea.

For over two thousand years, naturalists have proceeded on the basis of an infinite three-dimensional space, which endured by the summation of a succession of instants. Now they are told that there is no Nature, alive or dead, at any given instant, that duration is essential to existence, that events can be precisely located neither in space nor in time, and that everything is in a state of movement or flux. In short, they have to adjust their ideas to an entirely different set of physical presuppositions.

Current taxonomy is still dependent on the old presuppositions, and so long as it is concerned with the position and motion of organisms it continues to function fairly well, particularly when dealing with the present, or with apparently isolated events in the past. Difficulties arise when one attempts to fit organisms in locomotion into a framework which was not designed to receive them. The result is then a compromise, which distorts either the component representing motion or that representing locomotion. The amount of distortion is largely dependent on the skill and judgement of the taxonomer, but it is never negligible.

So long as the primary object of taxonomy ' is simply to provide a convenient and practical means by which zoologists may know what they are talking about and others may find out ' (Simpson, 1945, p. 13), the distortion may not be of great moment, particularly if one does not lose sight of the ' secondary but still essential aim that classification should be consistent with the most important thing that evolutionary taxonomists have to talk about, that is, with animal affinities ' (Simpson, *loc. cit.*). Nevertheless, the distortion, which is the result of an endeavour to discuss velocity in terms of position, remains, and its effects are illustrated in Simpson's classification of the horses. There the lineage which leads from *Hyracotherium* to *Equus* is divided among three sub-families, each of them containing segments of one or more side branches as well as of the main stem. The classification is the fruit of great experience and mature judgment, but its author had no course open to him other than to represent a single biological entity of one kind under the guise of three entities of another kind. In effect, orthodox taxonomy, of which Simpson's classification is a brilliant example, emphasizes the static side of biology, what I have earlier called the motion of the organism, and therefore fails to give adequate representation to the organism's velocity, evolution or locomotion.

Osborn's formal classification of the Proboscidea sums up the results of over forty years' study of one group of animals. It is not generally accepted because, to quote Simpson again (*op. cit.* p. 244), it ' is profoundly and irreconcilably different from any other that has ever been proposed. As Osborn recognized, [it] differs more from any of the contemporaneous classifications than these do from the system of Linnaeus.'

Osborn's method was to isolate as many narrowly defined ascending lineages as the evidence appeared to warrant, and to call each lineage a sub-family. Larger gaps in the record broke the lineages into larger sections, or ' genera ', and minor gaps broke up the ' genera ' into still smaller section or ' species '; there are other complications, but they are of less importance. The fundamental difference is that Osborn constructed the first classification of organisms in locomotion, and, although he does not appear to have been aware of the fact, the first classification at all conformable with the modern physical background of biology. For this reason the Osbornian principles are worthy of closer study than they have hitherto received, since it may be that they foreshadow the the taxonomy of the future. Evolutionary biology now has the evolutionary physical background it requires as a basic assumption, and sooner or later its primary discipline must adapt itself to the changed conditions.

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CONTRIBUTIONS TOWARDS THE FUNGUS FLORA OF UGANDA.— IX. THE UREDINALES OF UGANDA

By E. M. WAKEFIELD and C. G. HANSFORD.

In 1920 (*Kew Bull.* 1920, pp. 290–94) 65 species of Rust fungi were recorded from Uganda, mainly from collections made in the Kyagwe district by R. A. Dummer. Previous to this the only Uganda records found by us were *Aecidium Heteromorphae* A. L. Smith, published in a list of East African fungi collected by Scott Elliot (*Journ. Bot.* **33**, 1895) and a mention of *Puccinia glumarum* in the Fort Portal region by Mattirolo (*Il Ruwenzori*, 1909). The extensive collections made by the junior author during his tenure of the post of Government Mycologist and Plant Pathologist in Uganda have brought to light many species of Rusts hitherto undescribed, as well as adding to our knowledge of those already known from this region. Some of the earlier determinations have had to be revised, and during the course of the work corrections in the determinations of the host plants or alterations in their nomenclature have sometimes necessitated changes in the manuscript names first given to new species. Unfortunately some of these manuscript names were published (they are thus *nomina nuda*) in a list of the parasitic fungi of Uganda which appeared in the *East African Agricultural Journal* between 1937 and 1938. Such names should be disregarded.

In recent years much of the critical material has been examined by Dr. G. B. Cummins of Lafayette Agricultural Station, Purdue University, and many new species have been described by him in a series of papers in the *Bulletin of the Torrey Botanical Club.* Our sincere thanks are due to Dr. Cummins for his ready help and co-operation. All his determinations to date have been included in the present list. We are indebted also to Dr. G. R. Bisby of the Commonwealth Mycological Institute for assistance in many ways.

The arrangement of the genera in this list is in accordance with Dietel's classification of the Uredinales in the second edition of Engler and Prantl, *Die natürlichen Pflanzenfamilien*, Band 6, 1928. Within each genus the species are arranged alphabetically, but a host index is added to facilitate reference. A word of explanation is perhaps necessary as to the mode of citation of localities. The name of the district is given first, followed by the name of the exact locality. Thus ' Teso, Serere ' indicates that the specimen recorded was found at Serere in the district of Teso.

Type specimens of the species here described for the first time are deposited in the Herbarium of the Royal Botanic Gardens, Kew. The large number of species so far known only from Uganda is noteworthy, but is probably due only to the fact that no other region of tropical Africa has so far been so thoroughly explored for these fungi. There has recently been some evidence that some at least of the new species occur also in West Tropical Africa. About 38 per cent. of the Uganda Rusts are common to the Union of South Africa, where Uredinales have also been extensively collected.

MELAMPSORACEAE.

CRONARTIEAE.

PHAKOPSORA APODA (Har. & Pat.) Mains in Mycologia **30,** 45 (1938).

Hosts : *Pennisetum polystachyon* Schult. (=*P. setosum* of African authors), Tororo, Jan. 1929, *Hansford* 997 ; Bugwere, Pallisa, Jan. 1930, *Hansford* 1024 ; *Setaria aequalis* Stapf, Kampala, Feb. 1930, *Hansford* 1059. See Cummins in Bull. Torr. Bot. Club **72,** 206 (1945).

P. DESMIUM (Berk. & Br.) Cummins in Bull. Torr. Bot. Club, **72,** 206 (1945). *Cerotelium Gossypii* Arth., ibid. **44,** 510 (1917).

Hosts : *Gossypium* spp. (cultivated cotton), common ; Kyagwe, Kipayo, *Dummer* 2183 ; Kampala, Jan. 1938, *Hansford* 2334.

P. HANSFORDII Cummins in Bull. Torr. Bot. Club **70,** 523 (1943).

Hosts : *Alchornea cordifolia* Mull.-Arg., Kawanda, June 1939, *Hansford* 2474 ; Kawanda, Mar. 1940, *Hansford* 2564 (type) ; *Acalypha* sp., Kigezi, Gorge on Kinkizi track, Aug. 1937, *Hansford* 2152 p.p.

ANGIOPSORA HANSFORDII Cummins in Bull. Torr. Bot. Club **72,** 206 (1945).
Host : *Melinis tenuissima* Stapf, Elgon, Kyasoweri, Dec. 1933, *Hansford* 1714 (type).

CROSSOPSORA ANTIDESMAE-DIOICAE (Racib.) Arth. & Cummins in Philipp. Journ. Sci. **61,** 474 (1936).
Host : *Antidesma venosum* E. Mey., Kyagwe, Kipayo, June 1915, *Dummer* 2504 ; Kampala, Entebbe Road, June 1942, *Hansford* 3012.

Dummer 2504 was originally referred with some doubt as the uredospore stage of *Puccinia aequalis* Henn. It is however obviously the same as *Hansford* 3012, which has been determined by Dr. Cummins as Raciborski's species (see Bull. Torr. Bot. Club **72,** 207 (1945)).

C. FICI Arth. & Cummins in Philipp. Journ. Sci. **61,** 463 (1936).
Host : *Ficus capensis* Thunb., Kiagwe, Mukono, June 1942, *Hansford* 3051 (Cummins in Bull. Torr. Bot. Club **72,** 207 (1945)).

COLEOSPORIEAE.

COLEOSPORIUM CLEMATIDIS Barclay in Journ. Asiatic Soc. Bengal **59,** part 2, 89 (1890) ; *Caeoma Clematidis* Thuem. Myc. Univ. 539.
Hosts : *Clematis incisodentata* A. Rich., Kampala, Bombo Road, Oct. 1930, *Hansford* 1375 ; Kigezi, Gorge near Kambuga, Aug. 1937, *Hansford* 2162 ; *C. Wightiana* Wall., Kampala, Nov. 1922, *Small* 625 ; *Clematis* sp., Bugishu, Nkokonjeru, *Hansford* 792.

C. IPOMOEAE Burr. in Bull. Illinois State Lab. Nat. Hist. **2,** 217 (1885).
Host : *Ipomoea* sp., Kawanda, Mar. 1940, *Hansford* 2565 (det. G.B.C.).

MELAMPSOREAE.

MELAMPSORA ACALYPHAE Petch in Ann. Roy. Bot. Gard. Peradeniya **4,** 301 (1909).
Hosts : *Acalypha* sp., Butambula, Dec. 1930, *Hansford* 1414 ; Toro, *Hansford* 1478.

This is probably identical with *Phakopsora Hansfordii* Cumm. As Sydow has pointed out, the ' teleutospores ' described by Petch are the paraphyses.

M. EUPHORBIAE (Schub.) Cast., Obs. **2,** 18 (1843).
Host : *Euphorbia* sp., Elgon, Sabei, Dec. 1933, *Hansford* 1703.

M. JUNODII Doidge in Bothalia **2,** 158 and 199 (1926).
Hosts : *Vernonia amygdalina* Del., Kigezi, Rukingiri, Aug. 1937, *Hansford* 2171 ; *Vernonia* sp.,Entebbe Road, Mar. 1938, *Hansford* 2394.

No. 2171 was determined by Dr. G. R. Bisby, who notes that the uredospores reach a greater length than that described and that the paraphyses are coloured.

M. RICINI Pass. in Erb. Critt. Ital. ser. 2, fasc. 4, no. 684 (1878). *Melampsorella Ricini* (Biv.-Bern.) de Toni in Sacc. Syll. **7,** 596 (1888).
Hosts : *Ricinus communis* L., Kampala, Aug. 1927, *Hansford* 837 ; Teso, Katakwi, Aug. 1933, *Hansford* 1654.

PUCCINIACEAE.

HEMILEIEAE.

HEMILEIA BUNTINGII Wakef. & Hansford apud Dade in Kew Bull. 1940, p. 219.
Host : *Strophanthus hispidus* DC., Entebbe, *Small* 650.

The type specimen was from the Gold Coast, West Africa, on the same host. Further examination of the type material shows that the original description of the teleutospores requires some modification, and that probably immature uredospores were included. While the teleutospores are at first subglobose or ellipsoid, they do eventually become angular as in most species of *Hemileia*; further the wall is always smooth, not with a few warts as described. A revised description is as follows:

Teleutosporae immixtae, primitus subglobosae, ovatae vel ellipsoideae, demum angulatae, angulis obtusis protractis, omnino laeves, 22–28 × 18–26μ, statim germinantes.

The species differs from *H. Strophanthi* Rac. mainly in the uredospore characters, as described. From *H. Smallii* it is distinguished by the more scattered distribution of the uredosori on the surface of the leaf, and by the larger aculei on the uredospore walls.

H. CHLOROCODONIS H. & P. Syd. in Ann. Mycol. **11,** 55 (1913).
Host: *Chlorocodon Whiteii*, Hook. f., Mulange, Oct. 1919, *Dummer* 4280 (II and III).

H. DIOSCOREAE-ACULEATAE Rac., Crypt. Paras. Java Exs. No. 37. *Uredo Dioscoreae-aculeatae* Rac., Paras. Alg. u. Pilz. Jav. **1,** 30 (1900).
Host: *Dioscorea* sp., Kyagwe, Kirerema, *Dummer* 619 (II).

H. HANSFORDII Syd. in Ann. Mycol. **37,** 198 (1939). (Fig. 1.)
Hosts: *Jasminum dichotomum* Vahl, Entebbe Road, June 1942, *Hansford* 3019,3159; Nov. 1943, *Hansford* 3231; *Jasminum* sp. (*J. dichotomum* vel. affin.), Entebbe Road Forests, Feb. 1938, *Hansford* 2389 (type); Kazi, near Kampala, Oct. 1936, *Hansford* 1917, Jan. 1938, *Hansford* 2322; *J. pauciflorum* Benth., Kisubi, Entebbe, Jan. 1945, *Hansford* 3664; *Jasminum* sp., Entebbe Road, Dec. 1940, *Hansford* 2953; Kawanda, June 1942, *Hansford* 3050.

When Sydow described the species he did not find teleutospores. In *Hansford* 1917 and 2322 teleutospores are present in some quantity. The description of these spores is as follows:

Teleutosporae immixtae, primitus complanato-ellipsoideae demum angulatae, angulis obtusis protractis et lateribus ideoque concavis, laeves, episporio 1μ crasso, 22–25 × 15–18μ, statim germinantes.

H. HARUNGANAE Cummins in Bull. Torr. Bot. Club **70,** 522 (1943).
Host: *Harungana madagascariensis* Poir., Kawanda, Aug. 1940, *Hansford* 2803.

H. HOLSTII Syd., Monogr. Ured. **3,** 213 (1915); *Uredo mkusiensis* Henn. in Engl. bot. Jahrb. **34**, 41 (1904).
Hosts: *Psychotria nigropunctata* Hiern, Entebbe Road, mile 13, April 1936, *Hansford* 1940; Entebbe Road, Nov. 1936, *Hansford* 1965; *Psychotria* sp., Kiagwe, Mulange, Mabira Forest, Mar. 1920, *Dummer* 4424.

H. OXYANTHI Cummins in Bull. Torr. Bot. Club **68,** 467 (1941).
Hosts: *Oxyanthus speciosus* DC., Entebbe Road, Aug. 1940, *Hansford* 2784 (type); *Oxyanthus* sp., Entebbe Road, Mar. 1938, *Hansford* 2395 (confirmed by G. B. Cummins).

H. PAVETTICOLA Maubl. & Roger in Bull. Soc. Myc. Fr. **54,** 48 (1938).
Host: *Pavetta ternifolia* Hook. f. ex Oliver, Kigezi, Rukingire, Aug. 1937, *Hansford* 2148; Kigezi, Mpalo, Aug. 1937, *Hansford* 2169 (both specimens determined by G. B. Cummins).

H. RUTIDEAE Cummins in Bull. Torr. Bot. Club **70,** 522 (1943).
Host: *Rutidea rufipilis* Hiern, Entebbe Road, Nov. 1940, *Hansford* 2915.

H. Scholzii (P. Henn.) Syd. in Engl. bot. Jahrb. **45,** 260 (1910).

Hosts: *Clerodendron Johnstonii* Oliver, Kigezi, Kabale, *Hansford* 971; Kigezi, Kabale, Kachwekano Farm, Aug. 1937, *Hansford* 2225; *Clerodendron capitatum* Schum. & Thonn., Kampala, *Hansford* 1361; *Clerodendron* spp., *Small* 415; Kyagwe, Namanyonyi, *Dummer* 2751; Entebbe Botanic Gardens, *Maitland* 229 p.p.; Masaka Road, mile 9, Nov. 1937, *Hansford* 2255; Entebbe Road, May 1936, *Hansford* 1844 p.p.

Hemileia Secamones Wakef. & Hansford, sp. n. (Fig. 2.)

Uredosori hypophylli, maculis parvis pallidis, venulis folii limitatis dense aggregati, e stomatibus exeuntes, minuti, ceracei, 80–140μ diam., aurantiaci dein expallentes. Uredosporae globosae, subglobosae vel late ellipsoideae, ubique minute aculeatae, $18–23 \times 15–22\mu$, episporio hyalino 1–1·5μ crasso. Teleutosporae non visae.

Hab. in foliis *Secamones* sp., Serere, Teso, Uganda, Oct. 1932, *Hansford* 1583.

The species is well characterized macroscopically by the small angular spots, bounded by the veins of the leaf, on the lower side of which the small, compact sori are closely crowded. The uredospores resemble those of *H. scitula* Syd., also described on a plant belonging to the family Asclepiadaceae, in that they are equally aculeate all over, and in this character the two species differ from other species of *Hemileia*. *H. scitula* differs in its slightly larger uredospores, with longer spines. In neither species have teleutospores yet been seen.

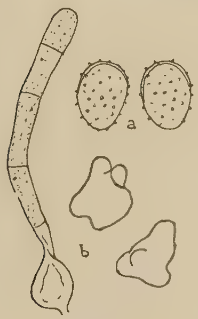

Fig. 1.
Hemileia Hansfordii Syd.
a. Uredospores. (×400).
b. Teleutospores, one germinating. (×400).

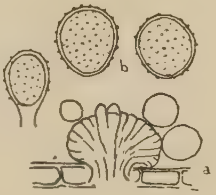

Fig. 2.
Hemileia Secamones Wakef. & Hansf.
a. Sorus. (×275.)
b. Uredospores. (×400.)

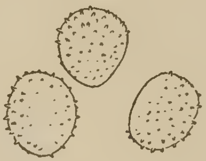

Fig. 3.
Hemileia Smallii Wakef. & Hansf.
Uredospores. (×400.)

Hemileia Smallii Wakef. & Hansford, sp. n. (Fig. 3.)

Sori uredosporiferi amphigeni, maculis parvis purpureo-brunneis insidentes, in greges 1–3 mm. diam. dense dispositi, brunneo-aurantiaci, sicco expallentes, pulverulenti. Uredosporae bilateraliter ovatae vel subglobosae, superficie convexa aculeatae, aculeis obtusis apicem versus ad. 1·5μ longis, parte inferiore plus minus applanata, laeves, hyalinae vel flavidae, episporio 1μ crasso, $25–30\,(–35) \times 23–28 \times 18–22\mu$. Teleutosporae non visae.

Hab. in foliis *Strophanthi Courmontii* Sacleux, Kampala, Uganda, *Small* 575 (*typus*); *Hansford* 1430; *Snowden* 697.

All three collections were made from the same individual tree. In early stages the leaves show spots 1 to 3 mm. in diameter, yellow to dull greenish-brown in colour. After the development of the sori the spots appear as brownish zones round the spore-masses. From *H. Buntingii* the species differs in the formation of definite leaf-spots and in the smaller and more crowded warts on the uredospores.

H. STROPHANTHI Rac. in Syd. Monogr. Ured. **3,** 217 (1914).
Host : *Strophanthus hispidus* DC., Entebbe, Sept. 1918, Maitland 319.

H. VASTATRIX Berk. & Br. in Gard. Chron. 1869, p. 1157.
Hosts : Native and cultivated coffee (*Coffea arabica* L. and *C. robusta* L.), common throughout Uganda : *Coffea liberica* Hiern., *Small* 362 ; *C. excelsa* Cheval., *Small* 363.

SKIERKEAE.

SKIERKA CONGENSIS P. Henn. in Ann. Mus. Congo ser. 5, **2,** 90 (1907).
Host: *Alchornea cordifolia* Mull.-Arg., Butambala, Sept. 1930, *Hansford* 1366 ; Masaka Road, mile 9, May 1936, *Hansford* 1790 ; Entebbe Road, mile 13, Nov. 1937, *Hansford* 2272.
No. 1366 was determined by H. Sydow, who states that the original host of this species was probably *Alchornea* and not *Dombeya,* as suggested by Hennings, nor *Macaranga,* as given in Sydow's Monogr. Ured.

CTENODERMA TODDALIAE (Petch) Syd. in Ann. Mycol. **17,** 103 (1919).
Host : *Toddalia aculeata* Pers., Kyagwe, Namanyonyi, *Dummer* 3054 ; Kampala, *Small* 511.
Following Mains, we retain this species in the genus *Ctenoderma* for the time being, since teleutospores have not been found. Other species of *Ctenoderma,* however, including the type species, have been shown by Mains (Mycologia **31,** 1939) to belong to the genus *Skierka.*

OLIVEAE.

OLIVEA SCITULA Syd. in Ann. Mycol. **35,** 251 (1937).
Host : *Vitex* sp., Teso, Serere, Oct. 1932, *Hansford* 1606 ; Dwoli, Hoima, April 1940, *Hansford* 2658 (det. G. B. Cummins).
No. 1606 was originally determined as *O. Petitiae* Arth., from which it differs however, in the absence of any leaf-spot, as well as in certain microscopic characters.

OCHROPSOREAE.

CEROTELIUM DAEDALOIDES Cummins in Bull. Torr. Bot. Club **70,** 521 (1943).
Host : *Clerodendron* sp. aff. *C. Bucholtzii,* Entebbe Road, Nov. 1940, *Hansford* 2917 ; Entebbe Road, Dec. 1940, *Hansford* 2939 (type).

C. FICI (Cast.) Arth. in Bull. Torr. Bot. Club **44,** 509 (1917).
Hosts : *Ficus Vallis-Choudae* Delile, Kampala, July 1930, *Hansford* 1314 ; *Ficus* spp., Kyagwe, Lumbwa, July 1916, *Dummer* 2870 ; Kyagwe, Kipayo, Jan. 1915, *Dummer* 1334 ; Kampala, 1922, *Small* 604 ; Entebbe Road Forests, Feb. 1938, *Hansford* 2373, 2393.

PHRAGMIDIEAE.

HAMASPORA LONGISSIMA (Thuem.) Koern. in Hedwigia **16,** 33 (1877).
Hosts : *Rubus* spp., Kyagwe, Mubango, Jan. 1915, *Dummer* 1343 (III) : Kampala; *Hansford* 1084 ; Mt. Elgon, Butambuli, Aug. 1934, *Hansford* 1731 (III), Kigezi, Kachwekano Farm, Aug. 1937, *Hansford* 2206 (II).

RAVENELIEAE.

Diorchidium Brachiariae Wakef. & Hansford, sp. n. (Fig. 4.)

Sori uredosporiferi sparsi, amphigeni vel caulicoli, flavidi dein obscure brunnei, pulverulenti, ellipsoidei, 250–500μ longi, epidermide fissa cincti. Uredosporae subglobosae, primo flavidae dein brunneae, 28–33 × 25–30μ,

episporio 1·5–2μ crasso minute sparseque echinulato, poris germinationis 2–3, plerumque 3, praedito. Sori teleutosporiferi conformes, interdum confluentes, atro-brunnei. Teleutosporae 26–35×34–48μ, brunneae, oblongo-ellipsoideae, utrinque rotundatae, septo plerumque verticali rarissime horizontali, ad septum constrictae, laeves, episporio 2·5–4μ crasso, ad apicem usque 8(–10)μ incrassato, poris germinationis apicalibus ; pedicelli hyalini, sursum vix flavescentes, ad 60μ longi.

Hab. in foliis culmisque *Brachiariae* sp., Serere, Teso, Uganda, Mar. 1933, *Hansford* 1631.

D. Tricholaenae Syd. in Ann. Mycol. **10,** 33 (1912).

Host : *Rhynchelytrum repens* (Willd.) C. E. Hubbard (=*Tricholaena rosea* Nees), Bunyoro, Dwoli Estate, Feb. 1928, *Hansford* 884 ; Kampala, *Hansford* 1037, *Snowden* 1403. Common everywhere.

Sphaerophragmium Acaciae (Cooke) Magnus in Ber. d.d. bot. Ges. **9,** 121 (1891).

Host : *Albizzia coriaria* Welw., Teso, Serere, Jan. 1933, *Hansford* 1622 (Cummins in Bull. Torr. Bot. Club **72,** 216 (1945)). The host was previously wrongly determined as *Cassia* sp.

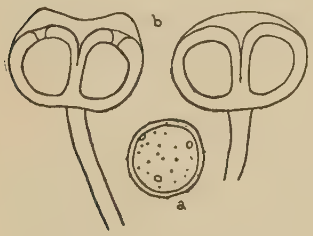

Fig. 4.
Diorchidium Brachiariae Wakef. & Hansf.
a. Uredospore. (×400.)
b. Two teleutospores. (×400.)

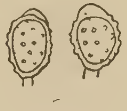

Fig. 5.
Uromyces Alysicarpi Wakef. & Hansf.
Teleutospores. (×400.)

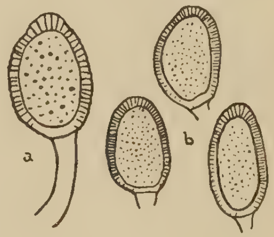

Fig. 6.
(*a*) *Uromyces Cluytiae* Kalchbr. & Cooke and (*b*) var. *minor* Wakef.
Teleutospores. (×400.)

S. Artabotrydis Doidge in Bothalia **4,** 232 (1941).

Hosts: *Artabotrys nitidus* Engl., Kazi, near Kampala, Jan. 1938, *Hansford* 2320; Entebbe Road, May 1938, *Hansford* 2409; *Artabotrys* sp. Kazi, near Kampala, Oct. 1936, *Hansford* 1915 ; Entebbe Road, Nov. 1937, *Hansford* 2286.

Ravenelia Baumiana P. Henn. in H. Baum, Bot. Ergebn. Kuneni-Sambesi Exped., 1903, p. 157.

Host : *Cassia goratensis* Fres., Karamoja, June 1940, *Hansford* 2717 (det. G. B. Cummins).

R. Bottomleyae Doidge in Bothalia **2,** 147 (1926).

Host : *Albizzia grandibracteata* Taub., Kawanda, July 1939, *Hansford* 2524. In the Bull. Torr. Bot. Club **72,** 215 (1945) Dr. Cummins has described an aecidial stage, previously unknown, from this material.

R. escharoides Syd. in Ann. Mycol. **10,** 440 (1912).

Host : *Acacia* sp.,Teso, Serere, Oct. 1932, *Hansford* 1603.

R. Hansfordii Cummins in Bull. Torr. Bot. Club **72,** 214 (1945).

Host :*Acacia* sp., Teso, Serere, Jan. 1933, *Hansford* 1616.

R. INDIGOFERAE Tranzsch. in Hedwigia **33,** 369 (1894).
Host : *Indigofera* sp. Mt. Elgon, Bukwa, Dec. 1933, *Hansford* 1698.

R. LAEVIOIDES Arth. & Cummins in Philipp. Journ. Sci. **61,** 470 (1936).
Host : *Indigofera* sp., Teso, Serere, Oct. 1932, *Hansford* 1601 ; Kigezi, Kinkizi, Aug. 1937, *Hansford* 2153. See Cummins in Bull. Torr. Bot. Club **72,** 215 (1945).

R. MARANGUENSIS (P.Henn.) Cummins in Bull. Torr. Bot. Club **72,** 125 (1945).
Uredo maranguensis P. Henn. in Engler, Pflanzenw. Ostafrikas 51 (1895).
Hosts : *Indigofera arrecta* Benth. ex. Harv. & Sond., Kigezi, Kisoro, Aug. 1937, *Hansford* 2197 ; *Indigofera* sp., Kyagwe, Lumbwa, April 1914, *Dummer* 2837 ; Mt. Elgon, Butandiga, *Hansford* 1737.

R. STUHLMANNII P. Henn. in Engl. Bot. Jahrb. **22,** 82 (1895).
Host : *Cassia* sp., Teso, Serere, Oct. 1932, *Hansford* 1576 ; *Hansford* 1784 p.p.

R. ZYGIAE Syd. in Ann. Mycol. **35,** 248 (1937) and **36,** 157 (1938).
Hosts : *Albizzia Brownei* Walp., Kyagwe, Kipayo, Sept. 1914, *Dummer* 1107 ; Kampala, Aug. 1930, *Hansford* 1335 ; *A. gummifera* (Gmel.) C. A. Sm., Kigezi, Lutobo, Aug. 1937, *Hansford* 2185 (det. G.B.C.) ; *A. zygia* Macbr., Kawanda, Kampala, June 1939, *Hansford* 2478 (det. G.B.C.).

Dummer 1107, which shows only teleutospores, was originally determined as *R. minima* Cooke (Kew Bull. 1920, p. 292). *Hansford* 1335 on the same host, however, shows both teleutospores and uredospores, the latter being like those of *R. zygiae*. Probably therefore the Dummer specimen is the same rust. *R. minima* and *R. zygiae* can scarcely be distinguished in the teleutospore stage, but the uredospores are oblong and apically thickened in *R. minima*, more elliptical and scarcely if at all thickened in *R. zygiae*.

UROPELTIDEAE.

UREDOPELTIS CONGENSIS P. Henn. in Ann. Mus. Congo ser. 5, **2,** 223 (1908).
Host : *Markhamia platycalyx* (Baker) Sprague, Kampala, *Small* 510 ; Kampala, June 1937, *Hansford* 2062 ; Kawanda, Aug. 1940, *Hansford* 2776.

PUCCINIEAE.

UROMYCES ALOES (Cooke) Magnus in Ber. d.d. bot. Ges. **10**, 48 (1892).
U. aloicola P. Henn. in Engl. bot. Jahrb. **14,** 370 (1891).
Host : *Aloe* sp., Kyagwe, Kipayo, June 1914, *Dummer* 903 ; Mt. Elgon, Butandiga, Aug. 1934, *Hansford* 1729.

Uromyces Alysicarpi Wakef. & Hansford. (Fig. 5.)

Status uredosporicus, *Uredo Alysicarpi* Doidge in Bothalia **2,** 194 and 212 (1926).

Sori amphigeni, sparsi, minuti, maculis nullis. Teleutosporae in uredosoris immixtae, latae ovatae, flavido-brunneae, 18–25 × 15–18μ, apice papilla hemispherica hyalina instructae, episporio 2–2·5μ crasso, verrucis sparsis obsito ; pedicelli breves, hyalini, decidui.

Hab. in foliis *Alysicarpi glumacei* (Vahl) DC., Kabaroni, Mt. Elgon, Uganda, Dec. 1933, *Hansford* 1713.

The teleutospores were found in a few sori only, developing from the middle of the uredospore pustule. Many of the sori in this material were parasitized by *Darluca*, which may account for the difficulty in finding teleutospores. Uredospore stages occurred also on *Alysicarpus rugosus* DC., Kyagwe, Kipayo, Sept. 1914, *Dummer* 1102 ; Toro, Kyabajazi, June, 1931, *Hansford* 1479 ; on *A. glumaceus* Kigezi, Kachwemba, Aug. 1937, *Hansford* 2183.

U. Andropogonis-annulati Syd. & Butl. in Ann. Mycol. **5,** 492 (1907).
Host : *Bothriochloa insculpta* (Hochst. ex. A. Rich.) A. Camus, Mt. Elgon, Bukwa, Dec. 1933, *Hansford* 1701 (det. G. B. Cummins).

U. aspiliicola Cummins in Bull. Torr. Bot. Club **72,** 208 (1945).
Host : *Aspilia asperifolia* O. Hoffm., Elgon, Kabaroni, Dec. 1933, *Hansford* 1723 (type).

U. bidenticola Arthur in Mycologia **9,** 71 (1917) ; *Uredo bidenticola* P. Henn. in Hedwigia **37,** 279 (1898).
Host : *Bidens pilosa* L., Kyagwe, Kipayo, Sept. 1914, *Dummer* 1101 ; Bugishu, Nkokonjeru, *Hansford* 790 ; Kigezi, Kabale, *Hansford* 931.
Dummer 1101 was originally referred to *Uromyces bidentis* Lagerh. following Sydow, but Arthur has shown that Sydow was in error in referring *Uredo bidenticola* Henn. to Lagerheim's species.

U. Chloridis Doidge in Bothalia **2,** 46 and 207 (1926).
Hosts : *Chloris myriostachya* Hochst., Karamoja, *Liebenberg* 1776 ; *C. pilosa* Schum. (=*C. breviseta* Benth.), Kampala, *Liebenberg* 1058 ; Kampala, *Hansford* 1040 (det. G. B. Cummins) ; *C. virgata* Sw., Karamoja, Kakamari, *Liebenberg* 1855.

U. Clignyi Pat. & Har. in Journ. de Bot. **14,** 237 (1900).
Hosts : *Andropogon abyssinicus* R. Br., Kigezi, Kabale, July 1928, *Hansford* 944 ; ? *A. pilosellus* Stapf, Kigezi, Kisoro, Aug. 1937, *Hansford* 2193, 2196 (det. G. R. Bisby) ; *Exotheca abyssinica* (Hochst. ex A. Rich.) Anderss., Kigezi, Kachwekano, Aug. 1937, *Hansford* 2222 ; *Bothriochloa insculpta* (Hochst. ex A. Rich.) A. Camus, Kawanda, Mar. 1941, *Hansford* 2989 (det. G. B. Cummins) ; Nov. 1942, *Hansford* 3097 ; July 1944, *Hansford* 3516 (det. G. R. Bisby).

U. Cluytiae Kalchbr. & Cooke in Grevillea **11,** 20 (1882).
Host : *Cluytia* sp., Mt. Elgon, Kabaroni, Dec. 1933, *Hansford* 1695.

U. Cluytiae Kalchbr. & Cooke, var. **minor** Wakef., var.n. (Fig. 6.)
Sori teleutospororiferi hypophylli, rotundati, umbrini, 0·5 mm. diam., concentrice dispositi, demum in greges ad 2 mm. diam. confluentes. Teleutosporae oblongae vel ellipsoideae, utrinque rotundatae, brunneae, 32–42 × 18–21μ, episporio subtiliter verrucoso, 2·5–3μ crasso, apice vix incrassato, papilla hyalina ornato, pedicello hyalino, usque 50μ longo.
Hab : in foliis *Cluytiae Richardianae* Mull.-Arg., Mt. Elgon, leg. *R. W. Stuckey*, *Hansford* 1244 (typus) ; et in foliis *Cluytiae abyssinicae* Jaub. & Spach, Kigezi, Nyarusanje, Aug. 1937, *Hansford* 2168.
Differs from the type in the paler, narrower, and much more finely warted teleutospores, and in the aggregate sori. No. 1244 seems so different from the type that at first it was thought to establish a new specific name for it, but No. 2168 seems to represent an intermediate form, with teleutospores in shape and size like those of the type of *U. Cluytiae*, but with the finer sculpturing of the epispore which is characteristic of this variety.

U. Commelinae Cooke in Trans. Roy. Soc. Edin. 1887, 342.
Hosts : *Commelina* spp., Kyagwe, Kirerema, July 1913, *Dummer* 164 (II) ; Kyagwe, Kiwafu, July–Aug. 1914, *Dummer* 919 (II) ; Kyagwe, Mubango, Mabira Forest, Jan. 1915, *Dummer* 1331 (II) ; Kampala, *Hansford* 1092 ; Teso, Serere, leg. *Chandler* no. 230, Dec. 1931, *Hansford* 1575 (III) ; Teso, Katakwi, Aug. 1933, *Hansford* 1656 (III). Common everywhere.

Uromyces Dactyloctenii Wakef. & Hansford, sp. n. (Fig. 7.)
Uredosori praecipue hypophylli, minuti, numerosissimi, rotundati vel elliptici, sparsi vel confluentes, cinnamomei, diu epidermide tecti dein ea fissa

cincti. Uredosporae globosae vel subglobosae, aurantio-brunneae, 25–28×22–24μ, vel 22–25μ diametro, episporio 1·5–2μ crasso, minute sparseque echinulato, poris germinationis aequatorialibus 3–4 instructo. Paraphyses adsunt, hyalinae vel flavidae, clavatae, supra ad 7–8μ diam. Teleutosori in foliis vetustis uredosoris intermixti, minuti, solidissimi, epidermide diu tecti, atri. Teleutosporae variabiles, subglobosae, ovatae vel piriformes, saepe e compressione angulatae, castaneae, ad apicem rotundatae vel truncatae, obscuriores, basi attenuatae, pallidiores, 25–27×18–20μ, episporio 2μ crasso, ad apicem usque 4–5μ incrassato. Pedicellus brevis, sursum flavidus, circa 25μ longus.

Hab. in foliis *Dactyloctenii aegyptii* (L.) Beauv., Katakwi, Teso, Uganda, Aug. 1933, *Hansford* 1653 (typus); Teso, Serere, May 1933, *Hansford* 1637; Serere, Jan. 1930, *Hansford* 1030 (II only); Hoima Road, leg. *H. B. Johnston*, 1933, *Hansford* 2247.

The minute, very compact teleutosori are characteristic, leaden-coloured while covered by the epidermis, later black. The teleutospores resemble those of *U. Peglerae* Pole Evans. Dr. Cummins has pointed out that this fungus may be the same as *U. dactylocteniicola* (Speg.) Lindquist (1943), but we have not been able to see the description of the latter.

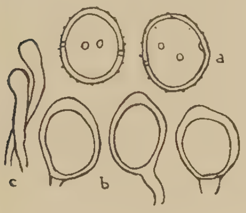

FIG. 7.
Uromyces Dactyloctenii Wakef. & Hansf.
a. Uredospores. (×400.)
b. Three teleutospores. (×400.)
c. Paraphyses. (×400.)

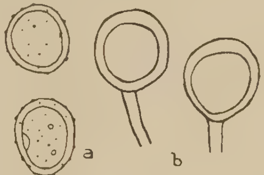

FIG. 8.
Uromyces Leptochloae Wakef.
a. Uredospores. (×400.)
b. Teleutospores. (×400.)

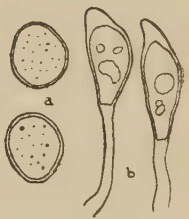

FIG. 9.
Uromyces notabilis Wakef.
a. Uredospores. (×400.)
b. Teleutospores. (×400.)

U. DIANTHI (Pers.) Niessl in Verh. Naturf. Ver. Brunn, **10,** 162 (1872).
Host: *Dianthus Caryophyllus* L., cultivated carnations, Kampala, *Hansford*; Kigezi, Kabale, *Hansford* 970.

U. DOLICHI Cooke in Grevillea **10,** 127 (1882).
Host: *Rhynchosia densiflora* DC., Mbarara, Oct. 1925, *Maitland* 879.

? U. ELEGANS (Berk. & Curt.) Lagerh. in Tromso Mus. Aarsheft., **17,** 25 (1895).
Host: *Trifolium* sp., Mt. Elgon, Butambuli, 10,000 ft., Aug. 1934, *Hansford* 1739.

Aecidium only present. The habit resembles that of the American species, the scattered aecidia being spaced fairly equally all over the leaf, running between the veins. The microscopic characters also agree.

U. ERAGROSTIDIS Tracy in Journ. Mycol 7, 281 (1893).
Hosts: *Eragrostis superba* Peyr., Teso, Serere, Jan. 1930, *Hansford* 1031; Jan. 1933, *Hansford* 1619; Kawanda, Mar. 1941, *Hansford* 2991; *E. Tef* (Zucc.) Trotter=*E. abyssinica* (Jacq.), Link., Kawanda, Mar. 1941, *Hansford* 2986; *E. kiwuensis* Jedw., Kigezi, Kabale, Aug. 1937, *Hansford* 2181 (II).

U. FABAE (Pers.) de Bary in Ann. sci. nat. ser. 4, **20,** 80 (1863).
Hosts: *Vicia Faba* L., Kigezi, Kabale, July 1928, *Hansford* 943; *Vicia sativa* L., Kigezi, Kabale, July 1928, *Hansford* 967; Aug. 1937, *Hansford* 2215; Kigezi, Kachwekano, Aug. 1937, *Hansford* 2209.

U. GERANII (DC.) Fr., Summ. Veg. Scand. 514 (1849).
Host : *Geranium simense* Hochst., Kigezi, Kabale, July 1928, *Hansford* 950 ; Kigezi, Kachwekano, Aug. 1937, *Hansford* 2208. Uredospores only in both specimens.

U. GLADIOLI P. Henn. in Hedwigia **34**, 326 (1895).
Host : *Gladiolus quartinianus* A. Rich., Mubendi, Kakumiro, Nov. 1922, leg. *G. T. Philpott, Small* 649 ; Kigezi, Rukingiri, Aug. 1937, *Hansford* 2160.

U. HARMSIANUS (P. Henn.) Doidge in Bothalia **2**, 22 & 207 (1926).
Hosts : *Crotalaria striata* DC. (?), Kampala, Jan. 1931, *Hansford* 1444 ; Teso, Serere, Jan. 1933, *Hansford* 1613 ; *C. intermedia* Kotschy, Kampala, Bombo Road mile 6, Oct. 1931, *Hansford* 1549 ; *Crotalaria* sp. Teso, Katakwi, Aug. 1933, *Hansford* 1648.
All collections show uredospores only.

U. HOBSONI Vize in Grevillea **4**, 115 (1876).
Hosts : *Jasminum dichotomum* Vahl, I on leaves and stems, leg. *R. W. Stuckey*, May 1930, *Hansford* 1239 ; *Jasminum* sp., Mt. Elgon, Kabaroni, Dec. 1933, *Hansford* 1710; Mt. Debasien, Karamoja, leg. *A. S. Thomas*, *Hansford* 1992 (I on stems, confirmed by Dr. G. R. Bisby, who found also teleutospores in old aecidial cups) ; Mt. Moroto, Karamoja, I on stems, leg. *A. S. Thomas*, *Hansford* 1997 ; Entebbe Road, Nov. 1936, *Hansford* 1963 ; Masaka, Lake Nabugabo, July 1937, *Hansford* 2127 (I on leaves); Kazi, near Kampala, Jan. 1938, *Hansford* 2319.

U. HYPERICI (Spreng.) Curt., Cat. Pl. N. Car. 123 (1867).
Hosts : *Hypericum Lalandii* Choisy, Kyagwe, Kirerema, Nov. 1916, *Dummer* 3017 ; *H. peplidifolium* Rich., Kigezi, Kabale, July 1928, *Hansford* 952.

U. HYPOXIDIS Cooke in Grevillea **10**, 127 (1882).
Host : *Hypoxis* sp. Kyagwe, Kijude, July 1915, *Dummer* 2508.

U. IPOMOEAE Berk. in Grevillea **11**, 19 (1882).
Hosts : *Convolvulaceae* (*Ipomoea*?), Kyagwe, Gagade, July 1915, *Dummer* 2874 (II and III) ; *Ipomoea* sp., Kigezi, Bufundi, July 1928, *Hansford* 930 ; Kampala, Bombo Road, *Hansford* 762 ; Bugishu, Nkokonjeru, Dec. 1926, *Hansford* 781 ; Elgon, Kyasoweri, Dec. 1933, *Hansford* 1683 ; Kigezi, Kachwekano Farm, Aug. 1937, *Hansford* 2213 ; *Ipomoea tenuirostris* Choisy, Kigezi, Kabale, Aug. 1937, *Hansford* 2219.
Nos. 2213 and 2219 were determined by Dr. Bisby. Both show uredospores only, which in 2213 were found to be 25–33 × 22–25μ with the wall 2–3μ thick, and 2 to 4 scattered germ-pores. These uredospores are longer than the measurements given by Dr. Doidge for South African material, but in *Dummer* 2874, which shows the characteristic teleutospores of *U. Ipomoeae*, uredospores up to 35μ long were observed.

Uromyces Leptochloae Wakef., sp. n. (Fig. 8.)

Sori teleutosporiferi hypophylli, oblongi, confluentes, atrobrunnei, pulverulenti. Uredosporae immixtae, subglobosae, ovatae vel ellipticae, laxe aculeolatae, flavidae, 21–23μ diametro, vel 23–27 × 20–22μ, episporio 2·5μ crasso, poris germinationis 6–8 sparsis instructo. Teleutosporae subglobosae, brunneae, laeves, apice rotundatae, 22–24 × 20–23μ, episporio 2–2·5μ crasso, apicem versus usque 7μ incrassato, pedicello hyalino, persistente, 20–25 × 5μ.
Hab. in foliis *Leptochloae obtusiflorae* Hochst., Tororo, Jan. 1929, *Hansford* 999 (typus) ; Teso, Bugondo Hills, Mar. 1933, *Hansford* 1628.

U. LEPTODERMUS Syd. in Ann. Mycol. **4**, 430 (1906) and **5**, 493 (1907).
Hosts : *Panicum maximum* Jacq., Teso, Serere, Dec. 1926, *Hansford* 783 ; Kampala, *Hansford* 980 ; *Panicum* sp., Entebbe Road, mile 13, Jan. 1930, *Hansford* 1135 ; *Brachiaria brizantha* (Hochst. ex A. Rich.) Stapf, Kampala,

Hansford 1063 ; Busoga, *Hansford* 1014 ; Mt. Elgon, Kyasoweri, Dec. 1933, *Hansford* 1697 ; *B. comata* (Hochst. ex A. Rich.) Stapf, Bugwere, Bukedea, *Snowden* 1202 ; *B. Kotschyana* (Hochst. ex Steud.) Stapf, Teso, Serere, Dec. 1926, *Hansford* 808 ; *Hansford* 1035 ; Busoga, Iganga, Jan. 1930, *Hansford* 1019 ; Ankole, leg. *Snowden, Hansford* 1400 ; *B. semiundulata* (Hochst. ex A. Rich.) Stapf, Mt. Elgon, Kyasoweri, Dec. 1933, *Hansford* 1717 ; *Urochloa panicoides* Beauv. (=*U. helopus* Stapf), Bugwere, *Snowden* 1130 ; *Setaria pallidefusca* (Schum.) Stapf & Hubbard (=*S. rubiginosa* Miq.), Kampala, Jan. 1930, *Hansford* 1051 (det. G. B. Cummins) ; Kigezi, Kisoro, Aug. 1937, *Hansford* 2192 ; Kigezi, Kabale, Aug. 1937, *Hansford* 2228 (det. G. B. Cummins) ; *S. verticillata* (L.) Beauv., Kampala, Jan. 1930, *Hansford* 1043 (det. G. B. Cummins) ; Kigezi, Kabale, Aug. 1937, *Hansford* 2230 (det. G. B. Cummins).

U. LINEARIS B. & Br. in Journ. Linn. Soc. **14,** 92 (1873).
Host : *Panicum repens* L., Kawanda, Nov. 1942, *Hansford* 3105 (det. G. B. Cummins).

U. MELANTHERAE Cooke in Grevillea **10,** 127 (1882).
Hosts : *Melanthera Brownei* Sch. Bip., Kyagwe, Kipayo, Aug. 1914, *Dummer* 920 ; *Melanthera* sp., Kyagwe, Namanyonyi, Dec. 1915, *Dummer* 2753 ; *M. pungens* Oliv. & Hiern, Teso, Katakwi, Aug. 1933, *Hansford* 1649.

U. MICROCHLOAE Syd. in Ann. Mycol. **1,** 15 (1903).
Host : *Microchloa indica* (L.) Beauv., Karamoja, Rom Mts. July 1930, *Liebenberg* 1842.

This specimen is referred here tentatively, but differs from Sydow's description in having the sori both amphigenous and on the culms. The wall of the teleutospore is not absolutely smooth, but slightly punctate, and is only 1μ thick. No uredospores are present in this material.

U. MUCUNAE Rabenh. in Hedwigia **17,** 62 (1878).
Host : *Stizolobium Deeringianum* Bort, Kampala, May 1936, *Hansford* 1801 ; Kampala, June 1937, *Hansford* 2105.

Uromyces notabilis Wakef., sp. n. (Fig. 9.)

Sori hypophylli, maculis perspicuis purpurascentibus insidentes. Sori uredosporiferi elliptici, diu tecti, 0·5–1 mm. longi. Uredosporae dilute cinnamomeae, fere hyalinae, ellipsoideae, 22–25 × 17–19μ, episporio 1μ crasso, sparse minuteque verruculoso, poris germinationis obscuris. Sori teleutosporiferi compacti, rotundati vel ellipsoideae, epidermide obscurata diu tecti. Teleutosporae multo variables, clavatae, inaequaliter ellipsoideae vel fusiformes, saepe curvulae, dilute cinnamomeae, 30–45 × 12–15μ, apice acuminato ad 10μ incrassato ; pedicellus brunneus spora obscurior, persistens, ad 50μ longus, 5–6μ crassus.

Hab ; in foliis *Kyllingae* sp., Kabaroni, Mt. Elgon, Uganda, Dec. 1933, *Hansford* 1725 (typus) ; 1726 (uredospores only).

No species of *Uromyces* has hitherto been recorded on *Kyllinga*. This rust is remarkable for the somewhat contorted and fusiform teleutospores, with pedicels darker in colour than the spore-body.

Uromyces Ocimi Hansford, sp. n. (Fig. 10.)

Sori teleutosporiferi caulicoli, saepe partibus matricis incrassatis insidentes, lineares, saepius usque 10 cm. confluentes et caulem circumdantes, mox erumpentes sed epidermide disrupta vestiti, atrobrunnei, compacti. Teleutosporae obovatae vel ellipticae, castaneo-brunneae, laeves, apice rotundatae vel conicae, basi late rotundatae, 33–45 × 19–24μ, episporio 2–4μ crasso, ad apicem usque 9μ incrassato, pedicello persistente, flavo, elongato, tenuiter tunicato, usque 160μ longo, 5–8μ lato.

Hab. in caulibus *Ocimi menthaefolii* Hochst., Kampala, *Hansford* 1487.

U. ORIENTALIS Syd. in Ann. Mycol. **5,** 490 (1907).
Hosts : *Indigofera polysphaera* Baker, Teso, Serere, leg. *P. Chandler* 232, *Hansford* 1574 ; *Indigofera* sp., Kampala, Bombo Road, mile 6, Oct. 1931, *Hansford* 1548 ; Mt. Elgon, Bukwa, Dec. 1933, *Hansford* 1702.

U. PEGLERAE Pole Evans in Ann. Mycol. **12,** 263 (1914).
Hosts : *Digitaria gazensis* Rendle, Ankole, Kagera River, *Snowden* 1340 ; *D. ternata* (Hochst. ex Steud.) Stapf, Kampala, Aug. 1928, *Hansford* 975 ; Kyagwe, Nagunga, *Hansford* 768 ; Mt. Elgon, Kyasoweri, Dec. 1933, *Hansford* 1692 ; Kigezi, Kisoro, Aug. 1937, *Hansford* 2191 (II and III) ; *Digitaria* sp., Teso, Serere, Aug. 1933, *Hansford* 1662 (III) ; *D. velutina* (Forsk.) Beauv., Kawanda, June 1940, *Hansford* 2725 (det. G.B.C.).
Except where indicated the specimens show uredospores only. These are very pale brown and may have up to 5 germ-pores.

U. PHASEOLI Wint. in Rabenh. Krypt.-Flora von Deutschl. **1,** 157 (1882). *U. appendiculatus* (Pers.) Link Obs. **2,** 28 (1816).

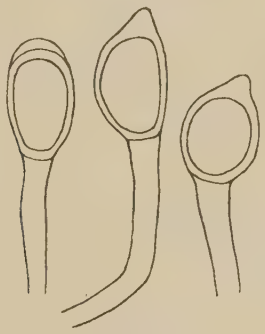

FIG. 10.
Uromyces Ocimi Hansf.
Teleutospores. (×400.)

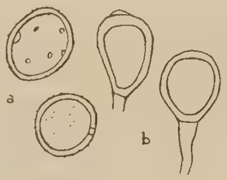

FIG. 11.
Uromyces Tragi Wakef. & Hansf.
a. Uredospores. (×400.)
b. Teleutospores. (×400.)

Hosts : *Phaseolus Mungo* L., Kyagwe, Kipayo, Oct. 1914, *Dummer* 1121 , Kampala, Dec. 1925, *Snowden* 974 ; *Vigna unguiculata* Walp., Busoga, Kamuli, 1913, *Small* 1 ; *Vigna* sp., Kampala, 1925, *Snowden* 977 ; *Phaseolus* sp., Kigezi, Kabale, Aug. 1937, *Hansford* 2231.

U. PISI Wint. in Rabenh. Krypt.-Flora **1,** 163 (1882).
Host : *Lathyrus* sp. (' Wedge Pea '), Kampala, Feb. 1938, *Hansford* 2374.

U. POLYGALAE Grove in Kew Bull. 1916, p. 269.
Host : *Polygala* sp., Kyagwe, Kiwafu and Kipayo, Mar. 1915, *Dummer* 2324.

U. POLYGONI-AVICULARIS Ramsb. in Trans. Brit. Mycol. Soc. **4,** 335 (1914). *U. Polygoni* (Pers.) Fuck. Symb. Myc. 64 (1869).
Host : *Polygonum tomentosum* Willd., Kigezi, Lake Bunongi, *Hansford* 945.

U. PRETORIENSIS Doidge in Bothalia **2,** 45 (1927), cfr. Cummins in Bull. Torr. Bot. Club **72,** 208, 1945.
Host : *Aneilema* sp., West Nile, Arua, July 1936, leg. *A. S. Thomas*, *Hansford* 1994 (det. G. R. B.).

U. PROËMINENS (DC) Pass in Rabenh. Fung. eur. 1795 (1874).
Host : *Euphorbia inaequilatera* Sond., Mt. Elgon, Kabaroni, Dec. 1933, *Hansford* 1719 (III) ; Mt. Elgon, Sipi, Dec. 1933, *Hansford* 1677 (I, II & III).

U. PSEUDARTHRIAE Cooke in Grevillea **10,** 127 (1882).
Host : *Pseudarthria Hookeri* Wight & Arn., Kampala, Sept. 1930, *Hansford* 1350, *Hansford* 1546 ; Teso, Serere, Oct. 1932, *Hansford* 1590, Masaka Road, Nov. 1937, *Hansford* 2262. Common everywhere.

U. PUNCTATUS Schroet. in Abh. Schles. Ges. **48,** 10 (1870).
Host : *Astragalus* sp., Mt. Elgon, Kyasoweri, Dec. 1933, *Hansford* 1685 (II only).

U. RUMICIS Wint. in Krypt.-Flora Deutschl. **1,** 145 (1882).
Host : *Rumex nepalensis* Spreng., Mt. Elgon, Kyasoweri, Dec. 1933, *Hansford* 1686 ; Kigezi, Kisoro, Aug. 1937, *Hansford* 2195 (det. G.R.B.).
Both specimens show only poor uredospores, and the determination is not at all certain.

U. PUSTULATUS Wakef. in Kew Bull. 1922, p. 163.
Host : *Bauhinia fassoglensis* Kotschy, Busoga, Kiterera, *Hansford* 2811 (det. G. B. Cummins, see Bull. Torr. Club **70,** 530, 1943).

U. SCHINZIANUS P. Henn. in Bull. Herb. Boiss. 2 ser., **6,** 702 (1906).
Host: *Bauhinia fassoglensis* Kotschy, Mt. Elgon, Bukwa, Dec. 1933 *Hansford* 1699.
This rust was originally determined by us as a new species, but we are informed by Dr. Cummins, to whom a portion was sent, that it is almost certainly *U. Schinzianus*, which was described from the uredospore stage only. A complete description has been published by Dr. Cummins in Bull. Torr. Bot. Club **72,** 208, 1945.

U. SECAMONES Wakef. in Kew Bull. 1917, p. 311.
Host : *Secamone platystigma* K. Schum., Kyagwe, near Namanyonyi, Oct. 1916, *Dummer* 3012.

U. STRIATUS Schroet. in Abh. Schles. Ges. **48,** 11 (1870).
Host : Cultivated Lucerne (*Medicago sativa* L.), Kyagwe, Mulange, Jan. 1920, *Dummer* 4420 ; Teso, Serere, Dec. 1931, *Hansford* 1509.

U. TENUICUTIS McAlp., Rusts of Australia, 87 (1906).
Hosts : *Sporobolus festivus* Hochst. ex A. Rich., Teso, Serere, June 1933, *Hansford* 1643; *S. pyramidalis* Beauv., Kigezi, Kabale, *Hansford* 953; Kampala, *Hansford* 974 ; Busoga, Iganga, Jan. 1930, *Hansford* 1018 ; Teso, Serere, Jan. 1930, *Hansford* 1032 ; Teso, Serere, Jan. 1933, *Hansford* 1614 (III) ; Kawanda, June 1940, *Hansford* 2726, July 1940, *Hansford* 2762 ; *Sporobolus* spp., Teso, Serere, Aug. 1933, *Hansford* 1660 (III) ; Toro, Fort Portal, *Liebenberg* 666.

Uromyces Tragi Wakef. & Hansford, sp. n. (Fig. 11.)
Sori uredosporiferi epiphylli, elliptici, primo epidermide tecti, demum aperti, epidermide disrupta cincti, 0·5–1 mm. longi, cinnamomei, pulverulenti. Uredosporae ovatae vel subglobosae, 19–27μ diametro, pallide flavidae, episporio subtiliter denseque echinulato, 1μ crasso, poris germinationis 4–7 sparsis praedito. Teleutosporae post uredosporas in eisdem soris efformatae ; sori atrobrunnei, compacti. Teleutosporae ovatae vel irregulares, laeves, atrobrunneae, 22–30 × 16–23μ, episporio 1·5μ crasso, apice vix incrassato, pedicello persistente, hyalino, usque ad 25μ longo.
Hab. in foliis *Tragi Berteroni* Schult., Ruwenzori, Dec. 1925, *Maitland* 976.
Also found on specimens of the same grass from Kenya, namely Makindu, coll. *A. Linton*, Feb. 1905, and Northern Yarra Plain, *D. C. Edwards*, Jan. 1938.

U. TRANSVERSALIS Wint. in Flora **67,** 263 (1884).
Host : *Gladiolus* sp., Mt. Elgon, Kabaroni, Dec. 1933, *Hansford* 1707.

Puccinia Abutili Berk. & Br. in Journ. Linn. Soc. **14,** 91 (1873).

Hosts : *Abutilon indicum* Sweet, Lango, Ayer and Bugishu ; Nkokonjeru, Dec. 1926, *Hansford* 785 ; Teso, Serere, Oct. 1932, *Hansford* 1592 ; *A. longicuspe* Hochst., Kigezi, Lutobo, Aug. 1937, *Hansford* 2186 ; *A. mauritianum* Don, Ankole, Mbarara, July 1937, leg. *J. Purseglove, Hansford* 2142 ; *Abutilon* sp., Teso, Serere, Oct. 1932, *Hansford* 1592 ; *Malvaceae*, indet., Kyagwe, Kipayo, Nov. 1914, *Dummer* 1304.

Puccinia Aframomi Hansford, sp. n. (Fig. 12.)

Sori uredosporiferi hypophylli, maculis minutis luteobrunneis insidentes, minuti, rotundati, diutius epidermide tecti, seriatim in lineas longas inter venulas dispositi. Uredosporae ellipticae, piriformes vel oblongae, melleo-flavidae, laxe aculeatae, 22–35 × 14–18μ, episporio 1·5–2·5μ crasso, poris germinationis duabus aequatorialibus praedito. Sori teleutosporiferi minuti, immixti, primo pallidi dein obscuriores, compacti. Teleutosporae clavatae, laeves, pallidae, fere hyalinae, apice rotundatae, non incrassatae, medio vix constrictae, basi attenuatae, 30–43 × 11–17μ (av. 35 × 15μ), episporio 1μ crasso ; pedicellus hyalinus, brevis, ad 20μ longus. Teleutosporae statim germinantes.

Hab. in foliis *Aframomi* sp., Masaka Road, Nov. 1937, *Hansford* 2250 (II & III, typus) ; May 1931, *Hansford* 1474 (II) ; Kampala, Jan. 1938, *Hansford* 2350 (II).

The uredospores differ from those of *Uredo Aframomi* Har. & Pat. in shape, larger size, and deeper colour. The colour of the uredospores is distinctly yellowish or honey coloured when mature, while the teleutospores are very pale, almost hyaline.

P. africana Cooke in Grevillea **8,** 71 (1879).

Host : *Spilanthes Acmella* Murr., Kyagwe, Kirerema, July 1913, *Dummer* 163 ; Bugishu, Nkokonjeru, Dec. 1926, *Hansford* 814 ; Kampala, Nov. 1926, *Hansford* 740 ; Bunyoro, Dwoli Estate, Hoima, Feb. 1928, *Hansford* 880 ; Teso, Serere, Oct. 1932, *Hansford* 1598.

P. Allii Rudolphi in Linnaea **4,** 392 (1829).

Host : *Allium Cepa* Linn., Kigezi, Mparo, leg. *J. D. Snowden, Hansford* 1002.

P. andropogonicola Har. & Pat. in Bull. Mus. Hist. Nat. Paris, 1909, p. 198.

Hosts : *Hyparrhenia* sp., Teso, Serere, Jan. 1933, *Hansford* 1620 ; *Cymbopogon* sp., Teso, Serere, April 1933, *Hansford* 1632. See Cummins in Bull. Torr. Bot. Club **72,** 209 (1945).

P. Asparagi DC., Fl. Fr. **2,** 595 (1805).

Host : *Asparagus* sp., Karamoja, April 1940, *Hansford* 2686.

P. Aspiliae-latifoliae Cummins in Bull. Torr. Bot. Club **68,** 468 (1941).

Hosts : *Aspilia Kotschyi* Benth., Teso, Serere, Oct. 1932, *Hansford* 1596 ; *A. latifolia* Oliv. & Hiern. Jinja Road, Oct. 1931, *Hansford* 1552 ; Semuto Road, Dec. 1943, *Hansford* 1943 ; *Aspilia* sp., Kumi, Eastern Province, Nov. 1931, *Hansford* 1558.

All specimens show the uredospore stage, and the aecidium also is present in No. 1552.

P. aurata Syd. in Ann. Mycol. **2,** 349 (1904).

Hosts : *Microglossa densiflora* Hook. f., Kyagwe, Namanyonyi, Feb. 1917, *Dummer* 3139 ; *Microglossa* sp., Kyagwe, Kipayo, Sept. 1914, *Dummer* 1110 ; Kampala, Feb. 1928, *Hansford* 897 ; *M. Afzelii* O. Hoffm., Masaka Road, May, 1936, *Hansford* 1787.

This species closely resembles *P. aecidiiformis* Thuem., but the teleutospores are somewhat shorter and scarcely thickened at the apex.

P. Berkheyae Wakef. in Kew Bull. 1917, 312.
Host : *Berkheya Spekeana* Oliv., Kyagwe, Namanyonyi, Dec. 1915, *Dummer* 2752 (Type) ; Toro, Kyabajazi, June 1931, *Hansford* 1478 (III) ; Mt. Elgon, Kabaroni, Dec. 1933, *Hansford* 1724 ; Kigezi, Rukingiri, Aug. 1947, *Hansford* 2174 (III) ; Kigezi, Kachwekano Farm, Aug. 1937, *Hansford* 2220 (II, III).

P. Bottomleyae Doidge in Bothalia **3,** 498, 1939.
Host: *Aristida adscensionis* L., Teso, Katakwi, Aug. 1933, *Hansford* 1651; *A. hordeacea* Kunth, Karamoja, July 1930, *Liebenberg* 1775 ; *A. adoensis* Hochst., Kawanda, Nov. 1942, *Hansford* 3095.

P. Chloridis Speg. in Rev. Arg. Hist. Nat. **1,** 172 (1891).
Hosts : *Chloris Gayana* Kunth, Tororo, Jan. 1929, *Hansford* 1001 ; Kawanda, June 1940, *Hansford* 2724 ; July 1940, *Hansford* 2755 ; *C. pycnothrix* Trin., Kigezi, Kabale, Aug. 1937, *Hansford* 2180, 2214 ; *C. virgata* Sw., Busoga, Jinja, Sept. 1929, *Hitchcock* 24954 ; *Chloris* sp., Kampala, July 1936, *Hansford* 1897 ; also *Hansford* 972, 1040, 1229. Common.

P. Cnici-oleracei Pers. apud Desm. Cat. des Plant. omises, 24 (1823).
Host : *Carduus* sp., Kigezi, Kabale, July 1928, *Hansford* 946 ; Mt. Elgon, 10,000 ft., Aug. 1934, *Hansford* 1728.

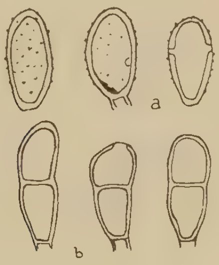

Fig. 12.
Puccinia Ajramomi Hansf.
a. Uredospores. (×400.)
b. Teleutospores. (×400.)

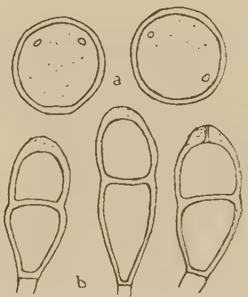

Fig. 13.
Puccinia Dummeri Wakef.
a. Uredospores. (×400.)
b. Teleutospores. (×400.)

P. Coreopsidis Wakef. in Kew Bull. 1918, p. 209.
Hosts : *Coreopsis* spp., Kyagwe, Kipayo, Sept. 1914, *Dummer* 1113 (type) ; Toro, Kyabajazi Estate, June 1931, *Hansford* 1477 ; Kigezi, Rukingiri, Aug. 1937, *Hansford* 2155 ; Bunyaraguru, Ankole, leg. *J. Purseglove, Hansford* 2293.

P. coronata Corda, Icon. Fungorum **1,** 6 (1837).
Host : *Helicotrichum lachnanthum* (Hochst. ex A. Rich.) C. E. Hubbard, Kigezi, Kabale, July 1928, *Hansford* 961 (II only). Determined by Dr. G. B. Cummins.

P. Cymbopogonis Mass. in Kew Bull. 1911, p. 224.
Host : *Cymbopogon citratus* (DC. ex Nees) Stapf, Entebbe, *R. Fyffe*, 1911 (type) ; Kampala, Jan. 1914, *Small* 7 (II).
This species differs from other rusts on *Cymbopogon* in the thick-walled uredospores, which are very closely and finely verruculose, with at times a striate appearance.

P. Cynodontis Delacr. ex Desm. in Crypt. Fr. ser. 2, no. 655 (1859).
Host: *Cynodon plectostachyus* (K. Schum.) Pilger, Fort Portal, *Hansford* 1006.

P. deformata Berk. & Curt. in Journ. Linn. Soc. **10,** 357 (1869).
Host : *Olyra latifolia* L., Butambala, Sept. 1930, *Hansford* 1371.
In this specimen the teleutosori are on the leaves, but otherwise in no way different from those of the type.

P. Dieramae Syd., Mon. Ured. **1,** 597 (1903).
Host: *Dierama* sp., Mt. Elgon, Madangi, Aug. 1934, *Hansford* 1738.

P. dimorpha Syd., Mon. Ured. **1**, 227 (1902).
Host: *Rubia cordifolia* Linn., Mt. Elgon, Kyasoweri, Dec. 1933, *Hansford* 1711.

Puccinia Dummeri Wakef., sp. n. (Fig. 13.)

Sori, sparsi, minuti, 0·5 mm. diametro, epi- vel hypophylli, interdum amphigeni, maculis nullis. Sori uredosporiferi brunnei, pulverulenti, epidermide lacerata cincti. Uredosporae globosae vel subglobosae, 27–30×30–35μ, episporio brunneo, minute echinulato, poris germinationis 3–4 praedito. Sori teleutosporiferi conformes, atrobrunnei, compacti. Teleutosporae castaneo-brunneae, ellipsoideo-oblongae vel clavatae, apice rotundatae vel acutiusculae, basi plerumque attenuatae, minute tuberculatae, medio non vel vix constrictae, 40–50(–62)×20–23μ, episporio 1·5–2μ crasso, apice leniter incrassato (usque 5–6μ).

Hab. in foliis *Echinopis amplexicaulis* Oliv., Kiagwe, Lumbwa, Uganda, Sept.–Oct. 1916, *Dummer* 3008 (typus) ; Kigezi, Rukingire, Aug. 1937, *Hansford* 2173 ; in foliis *Echinopis gigantei* Rich., Lango, Lira, Nov. 1931, *Hansford* 1564 ; *Echinopis* sp., Ankole, Lwasamaire, July 1937, *Hansford* 2145.

The species of *Puccinia* so far known on species of *Echinops* are obviously closely related, all having similar large brown uredospores, and teleutospores which when seen under a high power are minutely but indistinctly warted. *Dummer* 3008 was originally referred to *P. pulvinata* Rabenh. (see Kew Bull. 1920 p. 291), as a form with rather small spores. Examination of further material from Uganda has shown however that the tropical African rust on *Echinops* differs constantly from those of more temperate regions in certain points, so that it seems advisable to describe it as distinct. In the Uganda species the sori are smaller than in either *P. pulvinata* Rabenh. or *P. Echinopis* Syd., and the teleutospores are always thickened at the apex, with a somewhat paler cap. The minute tubercular sculpturing of the wall can be best seen at this paler apex. The teleutospores differ also from those of both the species mentioned in being usually narrowed below, so that the shape of the spore is clavate or sometimes almost subfusiform. In size the spores are smaller than those of *P. Echinopis*. In the type (*Dummer* 3008) the sori are epiphyllous, but in *Hansford* 1564 and 2173 they are hypophyllous, and in 2145 there are a few on either side of the leaf.

Puccinia elgonensis Wakef., sp. n. (Fig. 14.)

Sori hypophylli, oblongi vel lineares, 0·5–5 mm. longi. Sori uredosporiferi cinnamomei, epidermide cincti. Uredosporae late ellipsoideae, ovatae, oblongae vel subtriangulares, 35–40×24–30μ, episporio cinnamomeo, sparse aculeato, 1·5–2·5μ crasso, poris germinationis 4 aequatorialibus praedito. Sori teleutosporiferi atri, compacti. Teleutosporae clavatae, apice rotundatae, basim versus attenuatae, castaneae, medio parum constrictae, 35–45(–60)×16–18 (–20)μ, pariete 1μ crasso, apice 3–5μ incrassato, pedicello brevissimo.

Hab. in foliis *Setariae orthostichae*, K. Schum., Kyasoweri, Elgon, Uganda, Dec. 1933, *Hansford* 1694.

The uredospores of this species are similar to those of *P. Chaetochloae* Arth., but no paraphyses have been seen. The teleutospores are narrower than those of *P. Chaetochloae*, and also narrower than those of *P. Cenchri*. The pedicels are very short, and often appear to be lacking, since the spore breaks away from the basal cell easily. The teleutospores, which were first seen, were originally referred to *Puccinia Cameliae* (Mayor) Arth., but the uredospores are quite different, and moreover this fungus is certainly not an *Angiospora*, to which genus Mains has referred *P. Cameliae*.

Hansford 893 on *Setaria* sp., from Dwoli, Hoima, has similar teleutospores to those of *P. elgonensis*, but the uredospores seen with this specimen are slightly smaller, less inclined to vary in shape, and the germ-pores are not distinct. It is referred here with some doubt.

P. ERLANGEAE Grove in Kew Bull. 1916, p. 270.

Host: *Erlangea tomentosa* S. Moore, Kigezi, Bufundi, July 1928, *Hansford* 928 (type); Kampala, Mar. 1930, *Hansford* 1119.

In No. 1119 uredospores are present. These were not seen in the original material. The description is as follows: Uredospore sori hypophyllous, scattered on light-coloured areas, 0·5 mm. in diameter, round to oblong, yellowish-brown, pulverulent. Uredospores ovate to subglobose, pale yellow-brown, 22–30 × 18–23μ, epispore 1–1·5μ thick, closely echinulate; germ-pores not seen. Paraphyses present, numerous, curved, rather thick-walled, yellowish above, 40–50μ long.

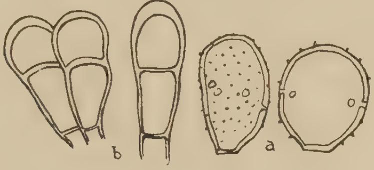

FIG. 14.
Puccinia elgonensis Wakef.
a. Uredospores. (×400.)
b. Teleutospores. (×400.)

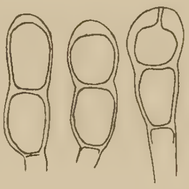

FIG. 15.
Puccinia Hansfordii Wakef.
Teleutospores. (×400.)

P. ERYTHRAEENSIS Pazschke apud P. Henn. in Engl. bot. Jahrb. **17,** 14 (1893).

Hosts: *Hyparrhenia cymbaria* (L.) Stapf, Bunyoro, Dwoli Estate, Feb. 1928, *Hansford* 876; *H. filipendula* (Hochst.) Stapf, Bunyoro, Dwoli Estate, Feb. 1928, *Hansford* 887; *H. Pilgeriana* C. H. Hubbard, Kigezi, Chahafi, Oct. 1929, leg. *Snowden, Hansford* 1907; Kigezi, Kisoro, Aug. 1937, *Hansford* 2200; *Cymbopogon afronardus* Stapf, Kampala, Sept. 1928, *Hansford* 976.

P. EXILIS Syd., Monogr. Ured. **1,** 481 (1903) var. HIBISCI Grove in Kew. Bull. 1916, p. 270.

Hosts: *Hibiscus rostellatus* Guill. & Perr., Masaka Road, mile 10, Nov. 1937, *Hansford* 2257; *Hibiscus* sp., Kyagwe, Kirerema, Mar. 1915, *Dummer* 2326; Entebbe Road, mile 13, Oct. 1931, *Hansford* 1545; Aug. 1940, *Hansford* 2786; Kawanda, Sept. 1940, *Hansford* 2837.

P. FIMBRISTYLIDIS Arth. in Bull. Torr. Bot. Club **33,** 28 (1906).

Host: *Fimbristylis exilis* Roem. & Schult., Teso, Katakwi, Aug. 1933, *Hansford* 1652.

P. GLUMARUM (Schum.) Erikss. & Henn., Die Getreideroste, 141 (1896).
Host : Wheat, cultivated, Toro, near Fort Portal, leg. *Roccati*, (Mattirolo, Duke of Abruzzi, in Il Ruwenzori, part. scientif. 1909). Wheat is not now grown in this district, and there is no other record of *P. glumarum* in Uganda.

P. GOUANIAE Holway in Ann. Mycol. **3,** 21 (1905).
Host : *Gouania* sp., Kyagwe, Kipayo, Jan. 1915, *Dummer* 1340 (II only).

P. GRAMINIS Pers., Synopsis, 228 (1801).
Host : Cultivated Wheat, Toro, 500 ft., *Small* 28 ; Bugishu, *Snowden* 527 ; Bugishu, Nkokonjeru, *Snowden* 1254 a ; Mubendi, Kakumiro, *Small* 596 ; Kigezi, *Snowden* 1267.

P. HANSFORDIANA Cummins in Bull. Torr. Bot. Club **70,** 523 (1943).
Host : *Senecio denticulatus* Engl., Kigezi, Kachwekano Farm, 6000 ft. Aug. 1937, *Hansford* 2227 (type).

Puccinia Hansfordii Wakef. (Fig. 15.)
Sori teleutosporiferi hypophylli, maculis flavidis indeterminatis insidentes, 1·5 mm. diam., aggregati, subinde confluentes, compacti, pulvinati, castaneo-brunnei. Teleutosporae elongatae, subclavatae, laeves, apice rotundatae vel subacuminatae, basi attenuatae, medio constrictae, flavidae, 45–58 × 15–20μ, episporio 1·5–2μ crasso, apicem versus usque 5–7μ incrassato, pedicello hyalino circa 20μ longo.
Hab. in foliis *Vernoniae* sp., Kampala, Bombo Road, Uganda, Nov. 1926, *Hansford* 754.
This is a Lepto-form like *P. vernoniicola* P. Henn., and *P. Le Testui* Maubl. From the former it differs in the darker sori and teleutospores and the marked thickening at the apex of the spore. From *P. Le Testui* it differs in the thinner-walled and narrower teleutospores, which are also paler in colour than the Uganda specimen of *P. Le Testui*.

P. HENNOPSIANA Doidge in Bothalia **2,** 118 and 202 (1926).
Hosts : *Mariscus Sieberianus* Nees, Kyagwe, Kipayo, Oct. 1914, *Dummer* 1152 ; *Mariscus* sp., Kyagwe, Kipayo, Oct. 1914, *Dummer* 1120.

P. HETEROSPORA Berk. & Curt. in Journ. Linn. Soc. **10,** 356 (1869).
Hosts : *Abutilon* sp., Kyagwe, Kipayo, May 1914, *Dummer* 647 ; *Sida grewioides* Guill. & Perr., Ankole, Mbarara, leg. *J. T. Kennedy*, July 1937, *Hansford* 2140 ; *Sida rhombifolia* L., Kyagwe, Namilyango, *Dummer* 1488 ; *Sida urens* L., *Hansford* 995 ; *Sida* sp., Entebbe, lake shore, Mar. 1918, *Maitland* 253.

P. HOLOSERICEA Cooke in Grevillea **10,** 126 (1882).
Hosts : *Convolvulaceae*, Kyagwe, Kivuvu, Dec. 1914, *Dummer* 1319 ; *Ipomoea* sp., Kampala, Kololo, *Hansford* 749 (?) ; Mt. Debasien, Karamoja, Dec. 1936, leg. *A. S. Thomas*, *Hansford* 1993 (III) ; Entebbe Road, Feb. 1938, leg. *Chandler*, *Hansford* 2346.

P. HOSLUNDIAE Syd. in Deutsch. Zentr. Afrika Exped. 1907–8, **2,** 97 (1911) ; *P. Hoslundiae* Grove in Kew Bull. 1916, 270.
Hosts : *Hoslundia opposita* Vahl, Kigezi, Rukingire, Aug. 1937, *Hansford* 2165 (II) ; Kigezi, Kambuga Gorge, Aug. 1937, *Hansford* 2164 (I, II, III) ; *Hoslundia* sp., Kyadondo, Magige, *Dummer* 1312 ; Kampala, *Hansford* 1071.
In No. 2164 an aecidial stage is present, which was not seen by either Sydow or Grove. The characters of the aecidium are as follows :
Aecidia hypophyllous or caulicolous, on the leaves aggregated in small circular sori, on the stems forming more extended, elongated sori, cupular or shortly cylindrical, projecting up to 0·5 mm., pale in dried specimens. Cells of

peridium irregularly polygonal, 25–40 × 20–22μ, wall striately verrucose, 2μ thick, pale, almost hyaline by transmitted light. Aecidiospores subglobose or elliptical, hyaline, thin-walled, 20–28(–30) × 18–22μ, wall minutely and densely verrucose.

P. INCOMPLETA Syd. in Ann. Mycol. **10,** 261 (1912).
Host : *Andropogon Dummeri* Stapf, Kawanda, Mar. 1941, *Hansford* 2990 (see Cummins in Bull. Torr. Bot. Club **72**, 209 (1945)).

P. KAERNBACHII Arth. in Bull. Torr. Bot. Club **46,** 110 (1919).
Host : *Hyparrhenia dissoluta* (Steud.) C. E. Hubbard, Kawanda, July 1940, *Hansford* 2759 (det. G. B. Cummins).

Puccinia kakamariensis Wakef. & Hansford, sp. n. (Fig. 16.)

Maculae nullae ; sori amphigeni sed praecipue hypophylli. Sori uredosporiferi sparsi vel plus minusve aggregati, elliptici, pallidi, 0·25–1 mm. longi, pulverulenti, diutius epidermide tecti. Uredosporae subglobosae, piriformes vel ellipticae, hyalinae, 20–26 × 16–22μ, episporio circa 1μ crasso, minute sparseque echinulato, poris germinationis obscuratis sed ut videtur 2–3 aequatorialibus praedito. Sori teleutosporiferi sparsi, erumpentes, rotundati vel oblongi, 0·5–1 mm. longi, atrobrunnei, pulvinati, epidermide rupta cincti. Teleutosporae irregulares, ellipsoideae, oblongae vel e compressione angulatae, apice rotundatae vel subconicae, rarius truncatae, medio plus minusve constrictae, basi rotundatae vel paullo attenuatae, 35–44 × 19–27μ, episporio castaneo, laevi, 2·5–3μ crasso, ad apicem usque 7μ incrassato, pedicello persistente subhyalino ad apicem flavido, usque 150μ longo, interdum oblique vel lateraliter inserto.

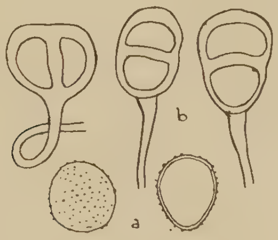

FIG. 16.
Puccinia kakamariensis Wakef. & Hansf.
a. Uredospores. (×400.)
b. Teleutospores. (×400.)

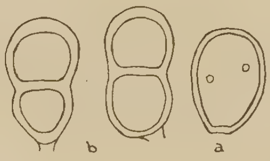

FIG. 17.
Puccinia kigeziensis Wakef. & Hansf.
a. Uredospores. (×400.)
b. Two teleutospores. (×400.)

Hab. in foliis vaginisque *Sporoboli* sp., Karamoja, Kakamari, Uganda, July 1930, *Liebenberg* 1774.

From *P. tosta* Arth. and *P. luxuriosa* Syd., which have both been recorded from South Africa, the present rust differs in the colourless uredospores. From *P. Vilfae* Arth. & Holw., which also has colourless uredospores, it differs in the wall of the uredospores not being thickened at the apex, and in the few germpores.

P. KALCHBRENNERI de Toni in Sacc. Syll. Fung. **7,** 645 (1888).
Hosts : *Helichrysum globosum* Sch. Bip., Kigezi, Kabale, July 1928, *Hansford* 955 ; Kampala, July 1931, *Hansford* 1490 ; *H. nudiflorum* DC., Kigezi, Mpalo, Aug. 1937, *Hansford* 2184 ; *H. undatum* Less., Kyagwe, Lumbwa, May 1917, *Dummer* 3233 ; *Helichrysum* spp., Kyagwe, Kipayo, Nov. 1914, *Dummer* 1192 ; Elgon, Sabei, Dec. 1933, *Hansford* 1681 ; Kigezi, Kachwekano Farm, Aug. 1937, *Hansford* 2207.

P. KAMPALENSIS Cummins in Bull. Torr. Bot. Club **72,** 213 (1945).
Host :*Wedelia oblonga* Hutch., Kampala, Feb. 1930, *Hansford* 1073.

Puccinia kigeziensis Wakef. & Hansford, sp. n. (Fig. 17.)

Sori uredosporiferi hypophylli, rarius etiam epiphylli, lineares, 0·5–1 mm. longi, sparsi, interdum confluentes, dilute brunnei, pulverulenti. Uredosporae ovatae vel angulato-subglobosae, e flavidis dilute brunneae, 29–35×25–28μ, episporio circa 2μ crasso, subtiliter sparseque verruculoso, poris germinationis 4–5 aequatorialibus interdum subpapillatis praedito. Teleutosporae in uredosoris orientes, ellipsoideae, medio non vel vix constrictae, laeves, apice rotundatae, brunneae, 28–39×17–25μ, episporio tenue, 1–1·5μ crasso apicem versus usque ad 5μ incrassato, pedicello brevissimo, hyalino, tenui, saepe deciduo, saepe oblique inserto.

Hab. in foliis *Setariae sphacelatae* (Schum.) Stapf & Hubb., Bufundi, Kigezi, Uganda, *Hansford* 934 (type) ; in foliis *S. verticillatae* (L.) Beauv., Kigezi, Bufundi, *Hansford* 948 (II).

In size both uredospores and teleutospores resemble those of *P. Chaetochloae* Arth., but paraphyses have not been observed, and the sori are not compact like those of *P. Chaetochloae.*

P. KRAUSSIANA Cooke in Grevillea **10,** 126 (1882).
Host : *Smilax Kraussiana* Meissn., Kyagwe, Kivuvu, Oct. 1914, *Dummer* 1116 ; Masaka Road, Aug. 1930, *Hansford* 1345 ; Entebbe Road, mile 13, Oct. 1931, *Hansford* 1541 p.p.; Rifle Range, Kiagwe, June 1938, *Hansford* 2442.

In *Dummer* 1116 and *Hansford* 2442 the teleutospore sori are markedly confluent, forming large pustules.

P. LATERITIA Berk. & Curt. in Journ. Acad. Nat. Sci. Phila., New Ser. **2,** 281 (1853).
Hosts : *Borreria Ruelliae* K. Schum., Kyagwe, Kipayo, Dec. 1913, *Dummer* 616 ; Ankole, Mbarara, July 1937, *Hansford* 2144 ; *B. sinensis* K. Schum., *Maitland* 307 ; *Borreria* sp., Kyagwe, Kirerema, *Dummer* 1470 ; Elgon, Sabei, Dec. 1933, *Hansford* 1720 ; Karamoja, June 1940, *Hansford* 2716.

P. LEONOTIDICOLA P. Henn. in H. Baum, Kunene Sambesi Exped. 157 (1903); *Aecidium Leonotidis* P. Henn. in Engler, Pflanzenwelt Ostafrikas 52 (1895).
Hosts : *Leonotis mollissima* Guerke, Mubendi, Mityana, Dec. 1931, *Hansford* ; Elgon, Kabaroni, Dec. 1933, *Hansford* 1706 ; *L. nepetaefolia* R. Br., Lango, Ayer, Dec. 1926, *Hansford* 786 ; Kampala, Aug. 1931, *Hansford* 1507 (III) ; Elgon, Sabei, Dec. 1933, *Hansford* 1705 ; Kigezi, Rukingire, Aug. 1937, *Hansford* 2170 (II) ; *Leonotis* sp., Kyagwe, Kipayo, Sept. 1914, *Dummer* 1108 ; Kyadondo, Magigye, *Dummer* 1482 (I) ; unlocalized, *Small* 443 (I).

P. LEPTOSPERMA Syd. Monogr. Ured. **1,** 557 (1903).
Host : *Drymaria cordata* Willd., Kyagwe, Kivuvu, Dec. 1915, *Dummer* 2740, Entebbe Botanic Gardens, July 1930, *Hansford* 1322.

P. LE TESTUI Maubl. in Bull. Soc. Myc. Fr. **22,** 71 (1906).
Host : *Vernonia* sp., Kyagwe, near Nkoko, July 1916, *Dummer* 2858.

P. LEUCADIS Syd. Monogr. Ured. **1,** 281 (1902).
Hosts : *Leucas martinicensis* R. Br., Kampala, Feb. 1930, *Hansford* 1068 ; Elgon, Bukwa, Dec. 1933, *Hansford* 1700 ; Kigezi, Rukingire, Aug. 1937, *Hansford* 2154 ; *L. calostachys* Oliv., Elgon, Kyasoweri, Dec. 1933, *Hansford* 1691.

P. LEVEILLEI Mont. in Gay, Fl. Chil. **8,** 41 (1852).
Hosts : *Geranium* sp., Bugishu, Nkokonjeru, Dec. 1926, *Hansford* 811 ; Elgon, Kyasoweri, Dec. 1933, *Hansford* 1693.

P. LIPPIICOLA Pat. & Har. in Bull. Soc. Mycol. Fr. **24,** 13 (1908). ?*P. lippiivora* Syd. in De Wildeman, Flore du Bas et Moyen Congo **3,** 11 (1909).

Hosts : *Lippia adoensis* Hochst., Kyagwe, Kipayo, Dec. 1914, *Dummer* 2301 ; Teso, Serere, Oct. 1932, *Hansford* 1580 ; *Lippia* sp., Elgon, Kyasoweri, Dec. 1933, *Hansford* 1690.

No. 1690 agrees very well with a South African specimen received under the name of *P. lippiivora* Syd., but all these specimens differ from the description of *P. lippiivora* in that the sori are grouped on dark brown spots, visible on both sides of the leaf, and are not ' minute ', being up to 1 mm. in diameter. The teleutospores are very variable in shape and size, in the Uganda specimens varying from 33 to 55μ in length and from 15 to 23μ in width. The pedicels also vary in length and may reach as much as 145μ. Mesospores are fairly frequent in *Hansford* 1580 but rare in 1690 and in *Dummer* 2301. It has not been possible to see the type specimens of either *P. lippiicola* or *P. lippiivora,* but we are inclined to think that they may all prove to belong to the same species. From all the South American species of *Puccinia* on *Lippia,* except *P. accedens* Syd., the Uganda rust differs in the smooth teleutospores. All the specimens here listed are obviously Lepto-forms, the teleutospores germinating in the sorus. *Dummer* 2301 was formerly referred to *P. accedens* Syd. (Kew Bull. 1920, p. 292), but it differs from that species not only in the less frequent mesospores but also in the longer (up to 50μ) teleutospores. Also *P. accedens* is said by H. S. Jackson to be a *Micropuccinia*. *P. lippiicola* was described from Africa and on the same species of *Lippia,* but the teleutospore pedicels are described as ' almost as long as the spores ', whereas in the Uganda form they are very long. There is no mention of mesospores in the description of *P. lippiicola,* nor of the method of germination, so that the present determination must remain provisional until the type can be examined.

Puccinia Loudetiae Wakef. & Hansford, sp. n. (Fig. 18.)

Sori uredosporiferi epiphylli vel hypophylli, lineares, brunnei, usque 10 mm. longi, epidermide disrupta cincti, pulverulenti, paraphysati. Uredosporae globosae, subglobosae vel ellipsoideae, brunneae, 25–35(–37) × 14–28μ, episporio 1·5–2μ crasso, minute denseque echinulato, poris germinationis 3–5 instructo. Paraphyses cylindricae vel vix capitatae, subhyalinae, usque 60μ longae et ad apicem 10–15μ latae. Sori teleutosporiferi epiphylli, sparsi vel in lineas elongatas confluentes, usque 10 mm. longi, brunnei, epidermide disrupta cincti, pulverulenti. Teleutosporae clavatae, dilute brunneae, apice rotundatae, saepe fere truncatae, basi subattenuatae, laeves, medio vix constrictae, septo aliquando obliquo, 28–42 × 13–18(–23)μ, episporio 1μ crasso, ad apicem haud incrassato, pedicello persistente, flavido, usque 30μ longo.

Hab. in foliis *Loudetiae phragmitoides* (Peter) C. E. Hubbard, Kampala, Uganda, *Hansford* 1174 (typus) ; etiam in foliis *Loudetiae arundinaceae* (Hochst. ex A. Rich.) C. E. Hubbard, Teso, Serere, Jan. 1930, *Hansford* 1029 ; Oct. 1932. *Hansford* 1599 ; Sept. 1933, *Hansford* 1666 ; *L. kagerensis* (K. Schum.) C. E. Hubbard, Entebbe Road, Mar. 1930, *Hansford* 1128, 1130 ; April 1936, *Hansford* 1763.

Except for the type material, *Hansford* 1174, all the collections show uredospores only. The sori are frequently heavily parasitized by *Darluca* sp., and teleutospores are rare. The latter are characterized by their rather pale brown colour and very thin walls. The rather large uredospores are as dark or even darker than the teleutospores.

P. MAGNUSIANA Korn. in Hedwigia **15,** 179 (1876).

Host : *Phragmites mauritianus* Kunth, Entebbe Road, *Hansford* 3146.

P. MENTHAE Pers. Syn. Fung. 227 (1801).

Host : *Mentha aquatica* L., Kampala, Aug. 1930, *Hansford* 1334.

P. MINUSSENSIS Thuem. var *africana* Cummins in Bull. Torr. Bot. Club **72,** 213 (1945).
Host : *Lactuca capensis* Thunb., Kampala, Sept. 1930, *Hansford* 1364 ; Kampala, Feb. 1930, *Hansford* 1066 (II only) ; Kampala, Nov. 1930, *Hansford* 1405, 1488, 1533 ; *Lactuca* sp., Kigezi, Kabale, Aug. 1937, *Hansford* 2211 (type) ; Ankole, Lwasamaire, Aug. 1937, *Hansford* 2156 (I, II).

As pointed out by Dr. Cummins this rust differs from typical *P. minussensis* in the small number of pores in the uredospores. In No. 2156 these uredospores are associated with an aecidium in structure like that of *P. minussensis.* On the other hand, *Hansford* 795, on *Lactuca capensis* from Nkokonjeru, bears an aecidium of the usual cupular type with a peridium, associated in circular sori. Unfortunately no other spore form is present in this specimen. Further work on the Lactuca rusts seems desirable.

P. NAKANISHIKII Diet. in Engl. bot. Jahrb. **34,** 585 (1904).
Hosts : *Cymbopogon excavatus* (Hochst.) Stapf, Kigezi, Kinkizi, Aug. 1937, *Hansford* 2149 ; *C. Martini* (Roxb.) W. Wats., ex India, *Hansford* 2988, 3101 ; *Cymbopogon* sp., Teso, Serere, Mar. 1933, *Hansford* 1626. (See Cummins in Bull. Torr. Bot. Club **72,** 209 (1945).)

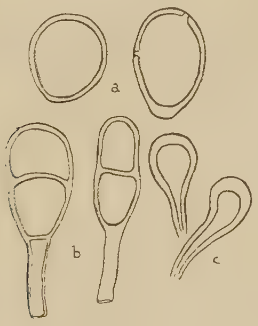

FIG. 18.
Puccinia Loudetiae Wakef. & Hansf.
a. Uredospores. (×400.)
b. Teleutospores. (×400.)
c. Paraphyses. (×400.)

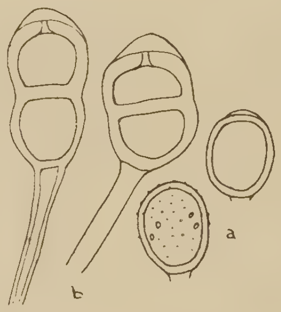

FIG. 19.
Puccinia Setariae-longisetae Wakef. & Hansf.
a. Uredospores. (×400.)
b. Teleutospores. (×400.)

P. NATALENSIS Diet. & Syd. in Hedwigia **38,** 130 (1899).
Host : *Lantana trifolia* L., Kyagwe, Kipayo, Nov. 1914, *Dummer* 1191 ; Teso, Serere, *Hansford* 798 ; Oct. 1932, *Hansford* 1579 ; Butambala, *Hansford* 1141 ; Kiagwe, Rifle Range, April 1940, *Hansford* 2682.

P. NATALENSIS var. EVANSII Doidge in Bothalia **2,** 82 (1926).
Hosts : *Lantana trifolia* L., Kigezi, Mpalo, Aug. 1937, *Hansford* 2187 ; *Lantana* sp., Kampala, Feb. 1930, *Hansford* 1074.

P. NECOPINA Grove in Kew Bull. 1916, 271.
Host : *Tristemma* sp., Kyagwe, Kipayo, *Dummer* 2325 ; Kampala, Bombo Road, *Hansford* 765.

P. OAHUENSIS Ell. & Ev. in Bull. Torr. Bot. Club **22,** 435 (1895). *P. Digitariae* Pole Evans in Ann. Bolus Herb. **2,** 111 (1907). See Cummins in Bull. Torr. Bot. Club **70,** 524–526 for discussion of the taxonomy and nomenclature of this rust.
Hosts : *Digitaria abyssinica* (Hochst.) Stapf, Kigezi, Kabale, Aug. 1937, *Hansford* 2235 (II) ; *D. marginata* Link, var. *fimbriata* Stapf, Lango, Ayer,

Hansford 809 ; *D. velutina* (Forsk.) Beauv. (=*D. digitata* Stapf), Bugwere, Terinyi, *Snowden* 536 ; *Digitaria* spp., Kyagwe, Kipayo, Aug. 1914, *Dummer* 949 ; Bunyoro, Dwoli Estate, Hoima, *Hansford* 892 ; Busoga, Iganga, *Hansford* 1020 ; Kigezi, Kabale, *Hansford* 932 ; Teso, Serere, Oct. 1932, *Hansford* 1600 (II and III) ; Teso, Katakwi, Aug. 1933, *Hansford* 1650 (II and III).

P. OCIMI Doidge in Bothalia **2,** 78 and 203 (1926).
Hosts : *Ocimum suave* Willd., Elgon, Kyasoweri, Dec. 1933, *Hansford* 1688 (III) ; Teso, Serere, Mar. 1933, *Hansford* 1627 (I) ; *Ocimum* sp., Kampala, Aug. 1930, *Hansford* 1333 (I).

P. OLDENLANDIAE P. Henn., in Engl. bot. Jahrb. **15,** Beibl. 33, 5 (1892).
Host : *Oldenlandia* sp., Kyagwe, Kipayo, Jan. 1915, *Dummer* 1349 ; Teso, Serere, Oct. 1932, *Hansford* 1581.

P. PENNISETI Zimmerm. in Ber. über Land- und Forstwirtsch. Deutsch Ostafr. 2, 16 (1904).
Hosts : *Pennisetum typhoides* (Burm.) Stapf. & Hubbard (=*P. typhoideum* L. C. Rich.), Bulemezi, Bukalasa, *Small* 594 ; Teso, Serere, Sept. 1934, *Hansford* 1745 ; Ankole, Mbarara, *Snowden* 1349, 1350 ; *P. clandestinum* Hochst., Kampala, *Hansford* 841 ; *Beckeropsis uniseta* (Nees) Stapf, Teso, Serere, Jan. 1933, *Hansford* 1615 (III).

P. PENTADICOLA Grove in Kew Bull. 1916, 271.
Hosts : *Pentas verticillata* K. Schum., Butambala, Dec. 1930, *Hansford* 1412 (II) ; *P. verticillata* var *pubescens* S. Moore, Kyagwe, Mubango, *Dummer* 1344 (type) ; *Pentas* sp., Kigezi, Kisoro, Aug. 1937, *Hansford* 2199 ; Kigezi, Kabale, Kachwekano Farm, Aug. 1937, *Hansford* 2224.

P. PENDATIS-CARNEAE Wakef. in Kew Bull. 1916, 74.
Host : *Pentas carnea* Benth., Kyagwe, Kipayo, Oct. 1914, *Dummer* 1123 (type) ; Bunyoro, Kinyala, April 1930, *Hansford* 1217.
Hansford 1217 shows uredospores, which were not present in the original material. Uredosori hypophyllous, on indefinite brown spots, visible on the upper surface, aggregated in small groups, rounded, dark brown, pulverulent. Uredospores subglobose, dark brown, shortly echinulate, 20–25μ in diameter, epispore 2–2·5μ thick ; germ-pores 3 to 4, scattered.

P. POLYGONI-AMPHIBII Pers., Syn. Fung. 227 (1801).
Hosts : *Polygonum acuminatum* H. B. & K., Kigezi, Kisoro, Aug. 1937, *Hansford* 2205 (II) ; *Polygonum* sp., Busoga, Junja and Ripon Falls, July 1913, *Dummer* 160 (II) ; *Oxygonum atriplicifolium* Martelli var. *sinuatum* Baker, Kyagwe, *Dummer* (*Small* 106) ; Kampala, *Hansford* 835, common.

P. PROPINQUA Syd. & Butl. in Ann. Mycol. **5,** 499 (1907).
Hosts : *Bothriochloa insculpta* (Hochst. ex A. Rich.) A. Camus, Butiaba, leg. *H. B. Johnston*, 1933, *Hansford* 2246. (See Cummins in Bull. Torr. Bot. Club **72,** 209 (1935).)

P. PRUNI-SPINOSAE Pers. Syn. Fung. 226 (1801).
Hosts : Cultivated Peaches (*Prunus persica* (L.) Batsch.), Bugishu, Nabumale, Aug. 1924, leg. *Snowden*, *Small* 671 ; Busoga, Iganga, *Snowden* 393 ; Toro, Fort Portal, *Hansford* 1008.

P. PURPUREA Cooke in Grevillea **5,** 15 (1876).
Hosts : *Sorghum verticilliflorum* (Steud.) Stapf, Kampala, *Hansford* 1056 ; cultivated *Sorghum*, common, Teso, Serere, *Snowden* 1001, *Small* 600, *Hansford*

P. ROTTBOELLIAE Syd. Monogr. Ured. **1,** 800 (1904).

Host : *Rottboellia exaltata* Linn. f., Lango, Ayer, Dec. 1926, *Hansford* 770, 787, 900, 1015, 1064 ; *Rottboellia* sp., Teso, Serere, Oct. 1932, *Hansford* 1589, common.

P. RUBIICOLA Syd., Monogr. Ured. **1,** 226 (1902).

Host : *Rubia cordifolia* L., Kigezi, Bufundi, July, 1928, *Hansford* 937.

This gathering agrees with the description of *P. rubiicola* in the characters of the teleutospores, but the sori are amphigenous. The species differs from *P. dimorpha* Syd. on the same host in the much smaller teleutospores, which in this specimen are not more than 45μ long.

P. RUFIPES Diet. in Engl. bot. Jahrb. **32,** 48 (1902).

Host : *Imperata cylindrica* (L.) Beauv. (=*I. arundinacea* Cyrilli), Bunyoro, Dwoli Estate, Feb. 1928, *Hansford* 879 (II only).

The rust is common all over Uganda wherever the host occurs, but only uredospores have so far been found.

Puccinia Setariae-longisetae Wakef. & Hansford, sp. n. (Fig. 19.)

Sori uredosporiferi amphigeni, sed saepius hypophylli, sparsi vel aggregati, minuti, elliptici, usuqe 2 mm. longi, cinnamomei, pulverulenti, epidermide disrupta cincti. Uredosporae e melleo dilute brunneae, globosae, vel subglobosae, 25–31μ diam., episporio 2–2·5μ crasso, sparse aculeato, poris germinationis 3–5 aequatorialibus instructo. Sori teleutosporiferi in vaginis culmisque, sparsi, lineares, confluentes, usque 5–6 mm. longi, epidermide diu tecti, demum partim expositi, pulverulenti, atri. Teleutosporae atrobrunneae, ellipsoideae vel oblongae, basi rotundatae vel attenuatae, medio leniter constrictae, apice rotundatae, conicae vel rarius truncatae, 35–50×22–28μ, episporio laevi, 2·5–3μ crasso, apice usque 11μ incrassato, pedicello subhyalino vel flavido, persistente, usque 110μ longo, subinde oblique vel lateraliter inserto.

Hab. in foliis, vaginis, culmisque *Setariae longisetae* Beauv., Kigezi, Kabale, Uganda, July 1928, *Hansford* 960 (typus) ; Kigezi, Mpalo, Aug. 1937, *Hansford* 2182.

The species is characterized by the pale brown uredospores with equatorially arranged germ-pores, and the thick-walled, long-pedicellate teleutospores, whose apex is thickened, often more or less conically, up to as much as 11μ. The uredospore sori on the leaves are not very conspicuous in the dried material, but the elongated, black teleutospore sori on sheaths and stems are easily seen. *P. kigeziensis* differs in the rather smaller, thinner-walled teleutospores, with short pedicels, and the more finely echinulate uredospores.

P. SONCHI Rob. ex Desm. in Ann. Sci. Nat. ser. 3, **11,** 274 (1849).

Hosts : *Sonchus Schweinfurthii* Oliv. & Hiern, Kigezi, Bufundi, *Hansford* 935 ; *Sonchus* sp., Kampala, *Hansford* 1069.

P. SORGHI Schw., Syn. Fung. Amer. Bor. 295 (1834) ; *P. Maydis* Bereng. in Atti VI Riun. Sci. Ital. Milano 475 (1884).

Host : Cultivated maize, Kyagwe, Mulange, June 1919, *Dummer* 4163 ; Kigezi, Kabale, *Hansford* 949 ; Bulimezi, Bukalasa, *Small* 597.

P. TABERNAEMONTANAE Berk. & Br. in Journ. Linn. Soc. **14,** 91 (1873).

Host : *Conopharyngia* sp., Gayaza, Feb. 1938, *Hansford* 2345 ; Gayaza Road, April 1940, *Hansford* 2644 ; Entebbe Road, Dec. 1940, *Hansford* 2944 ; *Conopharyngia usambarensis* Stapf, Entebbe Road, Dec. 1940, *Hansford* 2587 ; Nov. 1940, *Hansford* 2897.

P. Tecleae Pass. in Nuov. Giorn. Bot. Ital. **3,** 184 (1875).
Host: *Teclea nobilis* Del., Kyagwe, Mulange, Jan. 1919, *Dummer* 3931; Kazi, near Kampala, Oct. 1936, *Hansford* 1910; May 1937, *Hansford* 2029 (a); Bukalasa, April 1940, *Hansford* 2692; Busoga, Kiterera, Sept. 1940, *Hansford* 2815; Mabira Forest, *Snowden* 1007.

P. Thunbergiae-alatae P. Henn. in Engler, Pflanzenwelt Ostafrikas 50 (1895).
Host: *Thunbergia alata* Boj., Kyagwe, Namanyonyi, Jan. 1916, *Dummer* 2739 (II).

P. Tragiae Cooke in Grevillea **10,** 125 (1882).
Hosts: *Tragia brevipes* Pax, Elgon, Sabei, Dec. 1933, *Hansford* 1718; *Tragia* sp., Teso, Serere, Oct. 1932, *Hansford* 1595.

P. triticina Eriks. in Ann. Sci. Nat. ser. 8, **9,** 270 (1899).
Host: Cultivated wheat, Bugishu, Mt. Elgon, Nkokonjeru, Dec. 1927, *Snowden* 1254a; Kampala, *Small* 597, *Snowden* 662.

A specimen of *Thalictrum rhyncocarpum* Dill & Rich. collected in Aug. 1934 by Hansford in the Mt. Elgon region (*Hansford* 1730) bears aecidia on the stems and was suspected to be the aecidial stage of *P. triticina*. The aecidiospores however are consistently larger (19–33 × 17–23μ) than those of the wheat rust. This aecidium may belong to a rust on another grass of the same group, but without infection experiments it is impossible to allocate it.

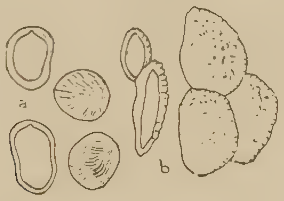

Fig. 20.
Endophyllum striatosporum Wakef.
a. Teleutospores. (×400.)
b. Cells of peridium. (×400.)

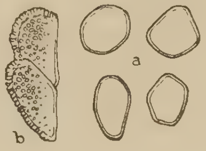

Fig. 21.
Aecidium Astrochlaenae Wakef. & Hansf.
a. Aecidiospores. (×400.)
b. Cells of peridium. (×400.)

P. ugandana Cummins in Bull. Torr. Bot. Club **70,** 562 (1943).
Host: *Jasminum* sp., Hoima Road, mile 20, *Hansford* 2672 (type).

P. vernoniicola P. Henn. in Engler, Pflanzenwelt Ostafrikas 50 (1895).
Host: *Vernonia* sp., Kampala, Jan. 1930, *Hansford* 1050; Kiagwe, Rifle Range, April 1940, *Hansford* 2679; Busoga, Kiterera, Sept. 1940, *Hansford* 2827.

P. versicolor Diet. & Holw. in Bot. Gaz. **24,** 28 (1897).
Hosts: *Heteropogon contortus* (L.) Beauv., Mt. Elgon, Butandiga, Aug. 1934, *Hansford* 1733 (II, III); Lake Albert Escarpment, 1933, leg. *H. B. Johnston* 951, *Hansford* 2248; *Themeda triandra* Forsk. var. *hispida* Stapf, Kigezi, Rukingire, Aug. 1937, *Hansford* 2175.

P. Zorniae McAlp., Rusts of Australia 172 (1906). *Uredo Zorniae* Berk. ex Cooke in Grevillea **20,** 110 (1892), non *U. Zorniae* Diet. in Hedwigia, **38.** 257 (1899).
Hosts: *Zornia diphylla* Pers., Kampala, Aug. 1931, *Hansford* 1527; Teso, Katakwi, Aug. 1933, *Hansford* 1657; *Zornia* sp., Kyagwe, Lumbwa, Sept. 1916, *Dummer* 3007.

Endophyllum (?) striatosporum Wakef., sp. n. (Fig. 20.)

Pycnidia non visa. Sori teleutosporiferi aecidiiformes, in foliis, caulibus fructibusque evoluti, in partibus leniter incrassatis insidentes, dense aggregati. Sori in foliis amphigeni sed praecipue hypophylli, in greges usque 7 mm. diam. dense dispositi, profunde immersi, cylindrici, angustati. Peridium album, usque 0·5 mm. emergens, margine lobato recurvato ; cellulae peridii firme conjunctae, elongato-rhomboideae vel polygonae, 25–35×20–22μ, pariete exteriore verruculoso, 3–4μ crasso, interiore grosse striato-verrucoso, 2·5–3μ. Teleutosporae angulato-subglobosae vel rhomboideae, 18–25×15–17·5μ, episporio hyalino, 2·5–3μ crasso, apice non vel vix incrassato, striis elongatis conspicuis ornato.

Hab. in foliis, caulibus fructibusque *Rhamni prinoides* L'Herit., Sabei, Elgon, Uganda, Dec. 1933, *Hansford* 1680.

Germination of the spores has not been observed, but the fungus is placed tentatively in *Endophyllum* because of its suggestive resemblance to *E. MacOwani* Pole Evans, described from South Africa on the same host-plant. The appearance of the sori is similar, but the spores are slightly smaller than those of *E. MacOwani* and are especially characterized by the striate appearance of the wall. This striation is due to thickenings in the form of ridges of varying length, running in the direction of apex to base of the spore. If the focus of the microscope is adjusted to the furrows between these ridges, the sculpturing of the spore-wall may appear somewhat reticulate.

PUCCINIOSIREAE.

PUCCINIOSIRA DISSOTIDIS Wakef. in Kew Bull. 1917, p. 313.

Hosts : *Dissotis incana* Triana, Kyagwe, Kipayo, *Dummer* 2157 ; *Dissotis* spp., Kyagwe, Namanyonyi, July 1916, *Dummer* 2865 ; Kyagwe, Sept. 1931, *Hansford* 1534 ; Elgon, Kabaroni, Dec. 1933, *Hansford* 1712 ; Kigezi, Kisoro, Aug. 1937, *Hansford* 2189.

CATENULOPSORA FLACOURTIAE Mundkur & Thirumalachar in Ann. Bot. n. s. **7,** 217 (1943).

Uredo Uguressae Petch in Ann. Roy. Bot. Gard. Peradeniya **4,** 303 (1909).

Host : *Flacourtia Ramontchi* L'Herit., Entebbe Road, Dec. 1943, *Hansford* 3266.

This specimen was determined by Dr. Cummins as *U. Uguressae.* Mundkur & Thirumalachar have since stated that their earlier differentiation was an error and that this uredo-form belongs to their species, *Catenulopsora Flacourtiae.* (See Imp. Mycol. Inst., Mycological Papers 16, p. 16, 1946.)

FORM-GENERA.

AECIDIUM ACANTHACEARUM Cooke in Grevillea **10,** 124 (1882).

Hosts : *Justicia flava* Vahl, Elgon, Kyasoweri, Dec. 1933, *Hansford* 1696 ; *J. uncinulata* Oliver var. *tenuicarpa* C. B. Cl., Kyagwe, Kipayo, May 1914, *Dummer* 649 ; *Small* 18, without locality ; *Justicia* spp., Kyagwe, Kipayo, June 1914, *Dummer* 900, 902 ; without locality, *Small* 19 ; Kampala, Mar. 1928, *Hansford* 900, 914 ; Elgon, Kabaroni, Dec. 1933, *Hansford* 1708.

A. AGERATI P. Henn. in Engler, Pflanzenwelt Ostafrikas 53 (1895).

Host : *Ageratum conyzoides* L., Kampala, Nov. 1926, *Hansford* 739.

Aecidium Astrochlaenae Wakef. & Hansford, sp. n. (Fig. 21.)

Aecidia hypophylla, maculis flavidis 2–7 mm. diam. insidentia. Maculae in folii superficie visae demum medio obscuriores leniter concavae. Aecidia dense gregaria, luteo-aurantiaca, leviter cupulata, peridio lacerato reflexo, 150–250μ diametro. Cellulae peridii laxe conjunctae, irregulariter rhomboideae, 22–30×16–20μ, pariete externo verrucoso, 3–6μ crasso, interiore dense minuteque verruculoso, 2–3μ crasso. Aecidiosporae irregulariter angulato-globosae vel ellipsoideae, aurantiacae, 16–21×12–61μ, episporio hyalino, dense minuteque verruculoso, 1μ crasso.

Hab. in foliis *Astrochlaenae* sp., Teso, Serere, Uganda, Oct. 1932, *Hansford* 1582.

A. Blumeae P. Henn. in Hedwigia **47,** 252 (1908).
Host: *Blumea lacera* DC., Kampala, July 1931, *Hansford* 1489.

A clerodendricola P. Henn. in Bot. Ergebn. Kunene-Sambesi Exped., 1903, p. 163.
Host: *Clerodendron* sp., Entebbe Road, July 1936, *Hansford* 1891.

A Cookeanum De Toni in Sacc. Syll. Fung. **7,** 822 (1888).
A. Loranthi Cooke in Grevillea **14,** 13 (1885).
Hosts: *Viscum* sp., Kangage Forest, Mar. 1915, *Maitland* 122; *Loranthus Woodfordioides* Schweinf., Mt. Elgon, Butandiga, Aug. 1934, *Hansford* 1734; *Loranthus* sp., Mt. Elgon, *Snowden* 1054.

Aecidium Crassocephali Wakef. & Hansford, sp. n. (Fig. 22.)

Aecidia hypophylla, rarius amphigena vel caulicola, saepius in greges latos dense disposita, maculis nullis, flavida, cupulata, 300–400μ diam., peridio albo revoluto inciso, cellulis peridii firme conjunctis, rhomboideis, 12–21×10–14μ, pariete exteriore 4μ crasso, irregulariter striato-verrucoso, interiore 2–3μ crasso, minute verruculoso. Aecidiosporae subhyalinae vel flavidae, irregulariter hexagoniiformes, 14–18×12–15μ, episporio 1·5μ crasso, subtiliter denseque verruculoso.

Hab. in foliis caulibusque *Crassocephali crepidioidis* (Benth.) DC., Busoga, Terinyi Ferry, Nov. 1931, *Hansford* 1561.

Also seen on the same host from the Gold Coast, and on *C. cernuum* from Sierra Leone.

A. Crotalariae P. Henn. in Engler, Pflanzenwelt Ostafrikas 52 (1895).
Hosts: *Crotalaria agatiflora* Schweinf., Kampala, *Small* 676, *Hansford* 1047; *Crotalaria* sp., Kampala, May 1915, *Small* 330.

A. Dichrocephalae P. Henn. in Monsunia **1**, 4 (1899).
Hosts: *Dichrocephala latifolia* DC., Kigezi, Bufundi, July 1928, *Hansford* 923; *Dichrocephala* sp., Bugishu, Nkokonjeru, *Hansford* 815.

A. Englerianum P. Henn. & Lind. in Bull. Herb. Boiss. **1**, 110 (1893).
Host: *Clematis* sp., Mt. Elgon, Kyasoweri, Dec. 1933, *Hansford* 1704; Virunga Mts., *Mildbraed* 1474.

A. entebbense Cummins in Bull. Torr. Bot. Club **72**, 221 (1945).
Host: *Phyllanthus discoides* Muell.-Arg., Entebbe Road, June 1942, *Hansford* 3016 (type).

A. Evansii P. Henn. in Engl. bot. Jahrb. **41**, 272 (1908).
Hosts: *Lippia* sp., Bugishu, Nkokonjeru, *Hansford* 780; Kampala, Bombo Road, *Hansford* 753; Bunyoro, Masindi, *Hansford* 1220; Elgon, Sabei, *Hansford* 1678, 1722. [See Cummins in Bull. Torr. Bot. Club **72**, 221 (1945)].

A. flavidum Berk & Br. in Journ. Linn. Soc. **14**, 95 (1873).
Host: *Pavetta* sp., Kyagwe, Kivuvu, July 1917, *Dummer* 3250.

An aecidium on *Pavetta crassipes* K. Schum. collected at Serere by P. Chandler in 1932 has spores which are intermediate in size between those of

A. flavidum and *A. transvaaliae* Pole Evans & Henn., but it differs from both species in causing marked deformation and swelling of the flower stalks. It has not at present been identified.

A. GARCKEANUM P. Henn. in Engl. bot. Jahrb. **14**, 372 (1891).
Host : *Hibiscus cannabinus* L., Teso, Katini, Nov. 1931, *Hansford* 1563 ; *Hibiscus* sp. cult., Kyagwe, Mugomba, Jan. 1915, *Dummer* 1346.

Aecidium Geniospori Wakef. & Hansford, sp. n. (Fig. 23.)

Aecidia hypophylla, maculis brunneis indeterminatis 1–7 mm. diam. insidentia, dense gregaria, cupulata, 150–200μ diam., peridio albo, revoluto inciso, cellulis peridii firme conjunctis, imbricatis, rhomboideis 24–35(–38) $\times$ 14–21μ, pariete exteriore crasse verrucoso, interiore subtiliter verruculoso. Aecidiosporae angulato-globosae subhyalinae, 15–19μ diam. episporio 1·5μ crasso, minute granulato.

Hab. in foliis *Geniospori paludosi* Baker, Kigezi, Kabale, Uganda, July 1928, *Hansford* 968 (typus) ; Kyagwe, Kivuvu, *Dummer* 370 ; Kampala district, Feb. 1930, *Hansford* 1085 ; Kampala, Bombo Road, mile 11, *Hansford* 760, 1413 ; Kigezi, Kachwekano Farm, Aug. 1937, *Hansford* 2223. Apparently common.

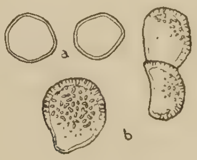

FIG. 22.
Aecidium Crassocephali
Wakef. & Hansf.
a. Aecidiospores. (×400.)
b. Cells of peridium. (×400.)

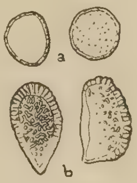

FIG. 23.
Aecidium Geniospori
Wakef. & Hansf.
a. Aecidiospores. (×400.)
b. Cells of peridium. (×400.)

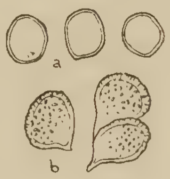

FIG. 24.
Aecidium Scopariae
Wakef. & Hansf.
a. Aecidiospores. (×400.)
b. Cells of peridium. (×400.)

A. HABUNGUENSE P. Henn. in H. Baum, Bot. Ergebnisse Kunene-Sambesi Exped., 160 (1903).
Host : *Solanum indicum* L., Kigezi, Kisoro, Aug. 1937, *Hansford* 2204 (det. G. R. Bisby).

A. HANSFORDII Cummins in Bull. Torr. Bot. Club **70**, 517 (1943).
Hosts : *Canthium vulgare* (K. Schum.) Bullock (=*C. golungense* Hiern), Entebbe Road, July 1939, *Hansford* 2486 ; Nov. 1940, *Hansford* 2925 (type) ; Kisubi, Entebbe, De. 1937, *Hansford* 2300 ; *Canthium* sp., Entebbe, *Maitland* 254.

A. HETEROMORPHAE A. L. Smith in Journ. Bot. Lond. **33**, 342 (1895).
Host : *Heteromorpha* sp., Ruwenzori, Yeria, *Scott Elliot* 184.

A. JUSTICIAE P. Henn. in Ann. Mus. Congo, ser. 5, **2**, 96 (1907).
Hosts : *Justicia flava* Vahl, Kawanda, Mar. 1940, *Hansford* 2566 ; *Justicia* sp., Kampala, Bombo Road, Nov. 1926, *Hansford* 763.

The spores are slightly larger than those in specimens determined as *A. acanthacearum* Cooke, but the species are otherwise similar. The aecidia on these hosts can be satisfactorily determined only when their life-histories are known.

A. MacOwanianum Thuem. in Flora, **58**, 380 (1875).
Hosts: *Conyza Hochstetteri* Sch. Bip. ex A. Rich., Ankole, June 1938, *Hansford* 2423; *Conyza* sp., Kigezi, Kabale, July 1928, *Hansford* 965; Kampala, Bombo Road, mile 6, Oct. 1931, *Hansford* 1547.

A. Micrococcae Syd. in Ann. Mycol. **36**, 159 (1938).
Host: *Micrococca mercurialis* Benth., Ankole, Bunyaraguru, Aug. 1937, *Hansford* 2238.

A. Mitracarpi Syd. in Ann. Mycol. **10**, 79 (1912).
Host: *Mitracarpum verticillatum* Vatke, Teso, Serere, Oct. 1932, *Hansford* 1578.

? A. Peucedani-raiblensis Maire in Oesterr. bot. Zeitschr. **57**, 330 (1907).
Host: *Peucedanum Karstenii* Engl., Ruwenzori, 12,500 feet, Aug. 1938, *J. W. Purseglove*, p. 273.

This fungus seems to agree fairly well with the description of *A. Peucedani-raiblensis*, otherwise known only from the Tyrol. The aecidia cause slight swelling and deformation of the leaf-petioles. The peridial cells have very thick walls, and the aecidiospores are hyaline, 23–30 × 20–23μ. The spores are larger than in any other aecidium known on *Peucedanum*, except the very incompletely described *A. Peucedani* Bacc. from Abyssinia. In the latter the spores are said to be verrucose, '20–40μ diam.', whereas the spores of the present fungus are only very finely punctate or almost smooth.

A. Phyllanthi P. Henn. in Engl. bot. Jahrb. **15**, Beibl. 33, 6 (1892).
Hosts: *Phyllanthus* spp., Kyagwe, Namanyonyi, Dec. 1916, *Dummer* 3055; Kyagwe, Mulange, April 1919, *Dummer* 4022.

The spores in these collections are rather smaller than in the type form, but they have even walls and therefore cannot be referred to *A. entebbense* Cummins. Further the pycnidia are amphigenous.

A. Pycnostachydis (Kalchbr.) Doidge in Bothalia **2**, 178 (1926).
Host: *Pycnostachys Dawei* N. E. Br., Kyagwe, Mugomba, *Dummer* 648.

Aecidium Scopariae Wakef. & Hansford, sp. n. (Fig 24.)

Aecidia hypophylla vel petiolicola, rarius caulicola. Sori in foliis rotundati, 1–1·5 mm. diam., in petiolis elongati. Aecidia minuta, 140–200μ diam., dense stipata, ex aurantiacis flavido-brunnea, peridio diutius occluso, demum cupulato, haud revoluto. Cellulae peridii subrhomboideae, firme conjunctae, 22–29 × 14–18μ, pariete exteriore verrucoso, 5–6μ crasso, interiore subtiliter verruculoso, 2μ crasso. Aecidiosporae angulato-globosae vel ellipsoideae, laeves, 14–17 × 13–16μ, episporio 1μ crasso, intus granulatae, melleae.

Hab. in foliis, petiolis caulibusque *Scopariae dulcis* L., Serere, Teso, Uganda, Oct. 1930, *Hansford* 1586.

A. Torae P. Henn. in Engl. bot. Jahrb. **34**, 42 (1904).
Host: *Cassia Tora* L., Lango, Bala, Dec. 1926, *Hansford* 813; Lango, Lira, Nov. 1931, *Hansford* 1562. Common.

A. Vangueriae Cooke in Grevillea **10**, 124 (1882).
Hosts: *Vangueria* sp., Bugishu, Bulago, July 1917, *Snowden* 521; *Rubiaceae* indet., Bugishu, Bupoto, Nov. 1916, leg. *Snowden*, *Small* 490; Kigezi, *Hansford* 2188.

A. Vernoniae-podocomae Doidge in Bothalia **2**, 173 (1926).
Host: *Vernonia* sp., Kampala, Mar. 1930, *Hansford* 1123; Kawanda, Kampala, June 1939, *Hansford* 2475 (det. G. B. Cummins).

A. VIGNAE Cooke in Grevillea **8**, 71 (1879).
Hosts : *Vigna unguiculata* Walp., Kampala, *Small*, 171 p.p., 128 ; *Vigna* sp., *Small* 101, 250 ; *Snowden* 975 ; *Hansford* 767 ; *Pueraria phaseoloides* Benth., Kampala, *Small* 127. Common.

A. VITIS A. L. Smith in Journ. Bot. Lond. **33**, 342 (1895).
Host : *Cissus* sp., Kampala, Bombo Road, Oct. 1931, *Hansford* 1374.

Uraecium Argomullerae Wakef., sp. n. (Fig. 25.)

Pycnidia subepidermalia, epiphylla, dense gregaria, circa 120μ alta, 90–100μ diametro. Aecidia epiphylla, maculis flavidis vel brunneis 4–7μ diametro insidentia, laxe aggregata, pustulata, 0·25–0·5 mm. diam., epidermide diu tecta, demum poro aperta. Aecidiosporae subglobosae, ellipticae vel piriformes, pallide cinnamomeae, sessiles, 27–35 × 23–27μ, episporio 1–1·5μ crasso, sparse aculeato.

Hab. in foliis *Argomullerae macrophyllae* Pax, Mubango, Mabiro Forest, Kyagwe, Uganda, Jan. 1919, *Dummer* 3937.

This rust is remarkable for the large, long-closed sori, which are covered by a dark brown, hard epidermis. The pycnidia occur in the centre of the leaf-spots and are easily overlooked. The aecidiospores are borne singly, not in chains, but appear to be sessile. Apparently no rust has so far been described on *Argomullera*.

UREDO ACHYRANTHICOLA Cummins in Bull. Torr. Bot. Club **72**, 219 (1945).
Host : *Achyranthes aspera* L., Kigezi, Kisoro, *Hansford* 2194.

U. ANTHISTIRIAE-TREMULAE Petch in Ann. Roy. Bot. Gard. Peradeniya **5**, 255 (1912).
Host : *Themeda triandra* Forsk., Bunyoro, Dwoli, April 1931, *Hansford* 886.
Differs from *Uredo themedicola* Cummins in the pale uredospores and in the presence of paraphyses. No teleutospores are present, but the rust may prove to be a species of *Angiopsora*.

U. ARTHRAXONIS-CILIARIS P. Henn. in Hedwigia **47**, 251 (1908).
Host : *Arthraxon Quartinianus* Nash, Bugishu, Nkokonjeru, Dec. 1926, *Hansford* 807 ; Masaka Road, mile 14, Oct. 1931, *Hansford* 1566 ; Mt. Elgon, Sipi, Dec. 1933, *Hansford* 1676 : Kigezi, Kisoro, Aug. 1937, *Hansford* 2202 ; Kigezi, Kabale, Aug. 1937, *Hansford* 2221 ; Kigezi, April 1940, *Hansford* 2626 ; Kawanda, Nov. 1942, *Hansford* 3096.

U. CENCHRICOLA P. Henn. in Ann. Mus. Congo, ser. 5, **2**, 223 (1908).
Host : *Cenchrus ciliaris* L., Kawanda, Mar. 1941, *Hansford* 2987. See Cummins in Bull. Torr. Bot. Club, **70**, 527 (1943).

U. CISSICOLA Cummins in Bull. Torr. Bot. Club **70**, 527 (1943).
Hosts : *Vitis quadrangularis* (L.) Wall. ex Baker, Busoga, Kiterera, Sept. 1940, *Hansford* 2813 (type) ; Kazi, near Kampala, Jan. 1938, *Hansford* 2330 ; *Cissus* sp., Entebbe Road, mile 15, July 1936, *Hansford* 1890.

U. CONVESTITA Syd. in Ann. Mus. Congo, ser. 5, **3**, 13 (1909).
Host : *Clerodendron cordifolium* A. Rich., Bunyoro, Kinyala, April 1930, *Hansford* 1225.

U. CORBICULOIDES Cummins in Bull. Torr. Bot. Club **72**, 219 (1945).
Host : *Grewia* sp., Teso, Serere, Mar. 1933, *Hansford* 1630 (type).

U. DIOSCOREAE-SATIVAE Syd. in Ann. Mycol. **10**, 271 (1912).
Host : *Dioscorea Beccariana* Martelli, Entebbe Road Forest, June 1937, leg. *P. Chandler*, *Hansford* 2102 (det. G. R. Bisby).

According to Dr. Cummins the sorus in this species is surrounded by a delicate peridium. We have been unable to find such a structure in any of the Uganda rusts on *Dioscorea*.

U. ENTENDOPHRAGMAE Cummins in Bull. Torr. Bot. Club, **70**, 527 (1943).
Host: *Entendophragma* sp., Entebbe Road, Dec. 1940, *Hansford* 2941 (type).

U. ERYTHRINAE P. Henn. in Ann. Mus. Congo, ser. 5, **2**, 224 (1908).
Host: *Erythrina tomentosa* R. Br., Kyagwe, Kipayo, Nov. 1914, *Dummer* 1311.

U. GOMPHRENAE Barclay in Journ. Asiatic Soc. Bengal **59**, part 2, 99 (1890).
Uromyces Cyathulae P. Henn. in Bull. Herb. Boissier, **1**, 107 (1893).
Hosts: *Cyathula globulifera* Moq., Kyagwe, Kipayo, Sept. 1914, *Dummer* 1109; Kigezi, Kachwekano Farm, Aug. 1937, *Hansford* 2229; *C. polycephala* Baker, Elgon, Sabei, Dec. 1933, *Hansford* 1682.

U. HYPOESTIS (Cooke) De Toni in Sacc. Syll. **7**, 850 (1888).
Host: *Hypoestes* sp., Elgon, Sabei, Dec. 1933, *Hansford* 1679.

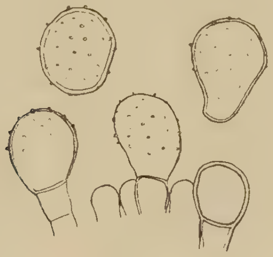

FIG. 25.
Uraecium Argomullerae Wakef.
Aecidiospores. (×400.)

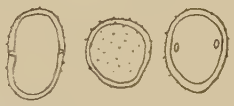

FIG. 26.
Uredo tesoensis Wakef. & Hansf.
Spores. (×400.)

U. INDIGOFERAE Doidge in Bothalia **2**, 195 & 213 (1926).
Hosts: *Indigofera procera* Schum. & Thonn., Kyagwe, Kijude, Jan. 1916, *Dummer* 2745; *Indigofera* spp., Kyagwe, Mubango, Feb. 1919, *Dummer* 3944; Kyagwe, Koja, Jan. 1928, *Hansford* 874; Hoima Road, mile 5, Aug. 1931, *Hansford* 1526; Masaka, L. Nabugabo, July 1937, *Hansford* 2118.
Apparently the most common rust on *Indigofera* in Africa.

U. KIGEZIENSIS Cummins in Bull. Torr. Bot. Club **70**, 527 (1943).
Host: *Eragrostis macilenta* Steud., Kigezi, Kabale, Aug. 1937, *Hansford* 2226 (type).

? U. KYLLINGIAE P. Henn. in Hedwigia **35**, 256 (1896).
Host: *Kyllinga* sp., Kigezi, Bufundi, July 1928, *Hansford* 924.
The uredospores of this specimen agree with those of Hennings' species, but, as Dr. Doidge has pointed out, the uredospores of *Puccinia kyllingicola* are similar. It is therefore not unlikely that the Uganda species will eventually be found to be the South African *Puccinia*, and possibly not the same as *Uredo Kyllingiae*, which was described from South America.

U. LONGAENSIS P. Henn. in H. Baum. Bot. Ergebn. Kunene-Sambesi Exped., 159 (1903).
Host: *Combretum* sp., Entebbe Road, Feb. 1938, *Hansford* 2388 p.p.

U. Melinidis Kern in Mycol. **30**, 550 (1938).
Hosts : *Melinis minutiflora* Beauv., Kigezi, Kisoro, Aug. 1937, *Hansford* 2201 ; *M. Maitlandii* Stapf & Hubbard, Kawanda, June 1940, *Hansford* 2727 ; Kawanda, Nov. 1942, *Hansford* 3108 ; *M. tenuissima* Stapf, Mt. Elgon, Sipi, Dec. 1938, *Hansford* 2563. See Cummins in Bull. Torr. Bot. Club **70**, 528 (1943).

U. palpigera Cummins in Bull. Torr. Bot. Club **72**, 221 (1945).
Host : *Inula acervata* S. Moore, Kigezi, Aug. 1937, *Hansford* 2150 (type).

U. Paspali-scrobiculati Syd. in Ann. Mycol. **4**, 444 (1906).
Host : *Paspalum Commersonii* Lam. (=*P. scrobiculatum* L. var. *Commersonii* Stapf), Bunyoro, Dwoli, Feb. 1928, *Hansford* 890.

U. Pergulariae Cummins in Bull. Torr. Bot. Club **72**, 220 (1945).
Host : *Pergularia* sp., Kiagwe, Rifle Range, June 1942, *Hansford* 3041.

U. perscita Cummins in Bull. Torr. Bot. Club **72**, 220 (1945).
Host : *Vernonia amygdalina* Delile, Kigezi, Rukingiri, Aug. 1937, *Hansford* 2171.

U. Phyllanthi-reticulati Petch in Ann. Roy. Bot. Gard. Peradeniya **7**, 295 (1922).
Host : *Phyllanthus* sp., Elgon, Butambuli, Aug. 1934, *Hansford* 1742.
This rust has brown capitate paraphyses and is probably a *Phakopsora*. It differs however from *Phakopsora Phyllanthi* Diet., in which the paraphyses are hyaline and curved.

U. Sesbaniae P. Henn. in Ann. Mus. Congo, ser. 5, **2**, 93 (1907).
Host : *Sesbania macrantha* Welw., Hoima Road, mile 8, Dec. 1930, *Hansford* 1436 ; *Sesbania* sp., Teso, Serere, Oct. 1932, *Hansford* 1594.

U. Stylosanthis P. Henn. in Hedwigia 38, (68), (1899).
Host : *Stylosanthes mucronata* Willd., Teso, Serere, Feb. 1933, *Chandler* 1122.

Uredo tesoensis Wakef., sp. n. (Fig. 26.)
Sori hypophylli et caulini, maculis brunneis indeterminatis insidentes, oblongi, ad 2 mm. longi, 0·5 mm. diametro, diu epidermide tecti, leniter elevati. Uredosporae subglobosae, ellipsoideae vel oblongae, flavido-brunneae, $20–30\times18–23\mu$, episporio $2{\cdot}5\mu$ crasso, sparse minuteque aculeato, poris germinationis duobus conspicuis equatorialibus instructo.
Hab. in foliis caulibusque *Kyllingae* sp., Serere, Teso, Uganda, June 1933, *Hansford* 1641 (typus), 1642.
The species differs from other rusts recorded on *Kyllinga* in the thick-walled brown uredospores, which somewhat resemble those of *Puccinia fuirenella* Doidge. In the collections of the Commonwealth Mycological Institute there is a rust on *Kyllinga peruviana* from Sierra Leone which has similar uredospores associated with a few *Puccinia* teleutospores. It seems likely therefore that the Uganda rust will eventually be found to be a *Puccinia*.

U. themedicola Cummins in Mycol. **33**, 151 (1941).
Host : *Themeda triandra* Forsk., Kawanda, July 1940, *Hansford* 2764 (determined by Dr. Cummins).

HOST INDEX.

Abutilon	*Puccinia Abutili* B. & Br. *Puccinia heterospora* B. & C.
Acacia	*Ravenelia escharoides* Syd. *R. Hansfordii* Cummins
Acalypha	*Melampsora Acalyphae* Petch *Phakopsora Hansfordii* Cummins

Achyranthes	*Uredo achyranthicola* Cummins
Aframomum	*Puccinia Aframomi* Hansford
Ageratum	*Aecidium Agerati* P. Henn.
Albizzia	*Ravenelia Bottomleyae* Doidge
	Ravenelia zygiae Syd.
	Sphaerophragmium Acaciae (Cooke) Magnus
Alchornea	*Phakopsora Hansfordii* Cummins
	Skierka congensis P. Henn.
Allium	*Puccinia Allii* (DC.) Rudolphi
Aloe	*Uromyces Aloës* (Cooke) Magn.
Alysicarpus	*Uromyces Alysicarpi* Wakef. & Hansf.
Amphilophis (see *Bothriochloa*)	
Andropogon	*Puccinia incompleta* Syd.
	Uromyces Clignyi Pat. & Har.
Aneilema	*Uromyces pretoriensis* Doidge
Anthistiria (see *Themeda*)	
Antidesma	*Crossopsora Antidesmae-dioicae* (Rac.) Arth. & Cummins
Argomuellera	*Uraecium Argomuellerae* Wakef.
Aristida	*Puccinia Bottomleyae* Doidge
Artabotrys	*Sphaerophragmium Artabotrydis* Doidge
Arthraxon	*Uredo Arthraxonis-ciliaris* P. Henn.
Asparagus	*Puccinia Asparagi* DC.
Aspilia	*Puccinia Aspiliae-latifoliae* Cummins
	Uromyces aspiliicola Cummins
Astragalus	*Uromyces punctatus* Schroet.
Astrochlaena	*Aecidium Astrochlaenae* Wakef. & Hansf.

Bauhinia	*Uromyces pustulatus* Wakef.
	Uromyces Schinzianus P. Henn.
Berkheya	*Puccinia Berkheyae* Wakef.
Bidens	*Uromyces bidenticola* Arth.
Blumea	*Aecidium Blumeae* P. Henn.
Borreria	*Puccinia lateritia* B. & C.
Bothriochloa	*Puccinia propinqua* Syd. & Butler
	Uromyces Andropogonis-annulati Syd. & Butler
	Uromyces Clignyi Pat. & Har.
Brachiaria	*Diorchidium Brachiariae* Wakef. & Hansf.
	Uromyces leptodermus Syd.

Canthium	*Aecidium Hansfordii* Cummins
	A. Plectroniae Cooke
Carduus	*Puccinia Cnici-oleracei* Pers.
Cassia	*Aecidium Torae* P. Henn.
	Ravenelia Baumiana P. Henn.
	R. Stuhlmannii P. Henn.
Cenchrus	*Uredo cenchricola* P. Henn.
Chloris	*Puccinia Chloridis* Speg.
	Uromyces Chloridis Doidge
Chlorocodon	*Hemileia Chlorocodonis* H. & P. Syd.
Cissus	*Aecidium Vitis* A. L. Smith
	Uredo cissicola Cummins
Clematis	*Aecidium Englerianum* P. Henn. & Lind.
	Coleosporium Clematidis Barcl.
Clerodendron	*Aecidium clerodendricola* P. Henn.
	Cerotelium daedaloides Cummins
	Hemileia Scholzii (P. Henn.) Syd.
	Uredo convestita Syd.
Cluytia	*Uromyces Cluytiae* Kalchbr.& Cooke and var. *minor* Wakef.
Coffea	*Hemileia vastatrix* B. & Br.
Combretum	*Uredo longaensis* P. Henn.
Commelina	*Uromyces Commelinae* Cooke
Conopharyngia	*Puccinia Tabernaemontanae* B. & Br.
Convolvulaceae	*Puccinia holosericea* Cooke
Conyza	*Aecidium Macowanianum* Thuem.
Coreopsis	*Puccinia Coreopsidis* Wakef.
Crassocephalum	*Aecidium Crassocephali* Wakef. & Hansf.
Crotalaria	*Aecidium Crotalariae* P. Henn.
	Uromyces Harmsianus (P. Henn.) Doidge
Cyathula	*Uredo Gomphrenae* Barcl.

Cymbopogon	*Puccinia andropogonicola* Har. & Pat.
	P. Cymbopogonis Massee
	P. erythraeënsis Pazschke
	P. Nakanishikii Diet.
Cynodon	*Puccinia Cynodontis* Delacr.
Dactyloctenium	*Uromyces Dactyloctenii* Wakef. & Hansf.
Dianthus	*Uromyces Dianthi* (Pers.) Niessl
Dichrocephala	*Aecidium Dichrocephalae* P. Henn.
Dierama	*Puccinia Dieramae* Syd.
Digitaria	*Uromyces Peglerae* Pole Evans
	Puccinia oahuensis Ell. & Ev.
Dioscorea	*Hemileia Dioscoreae-aculeatae* Rac.
	Uredo Dioscoreae-sativae Syd.
Dissotis	*Pucciniosira Dissotidis* Wakef.
Dolichandrone	*Uropeltis congensis* P. Henn.
Drymaria	*Puccinia leptosperma* Syd.
Echinops	*Puccinia Dummeri* Wakef.
Entendophragma	*Uredo Entendophragmae* Cummins
Eragrostis	*Uredo kigeziensis* Cummins
	Uromyces Eragrostidis Tracy
Erlangea	*Puccinia Erlangeae* Grove
Erythrina	*Uredo Erythrinae* P. Henn.
Euphorbia	*Melampsora Euphorbiae* (Schub.) Cast.
	Uromyces proëminens (DC.) Pass.
Exotheca	*Uromyces Clignyi* Pat. & Har.
Ficus	*Cerotelium Fici* (Cast.) Arth.
	Crossopsora Fici Arth. & Cummins
Fimbristylis	*Puccinia Fimbristylidis* Arth.
Flacourtia	*Catenulopsora Flacourtiae* Mundkur & Thirumalachar
Geniosporum	*Aecidium Geniospori* Wakef. & Hansf.
Geranium	*Puccinia Leveillei* Mont.
	Uromyces Geranii (DC.) Fr.
Gladiolus	*Uromyces Gladioli* P. Henn.
	Uromyces transversalis Wint.
Gossypium	*Phakopsora desmium* (B. & Br.) Cummins
Gouania	*Puccinia Gouaniae* Holw.
Grewia	*Uredo corbiculoides* Cummins
Harungana	*Hemileia Harunganae* Cummins
Helichrysum	*Puccinia Kalchbrenneri* de Toni
Helicotrichum	*Puccinia coronata* Corda
Heteromorpha	*Aecidium Heteromorphae* A. L. Smith
Heteropogon	*Puccinia versicolor* Diet. & Holw.
Hibiscus	*Aecidium Garckeanum* P. Henn.
	Puccinia exilis Syd. var. *Hibisci* Grove
Hoslundia	*Puccinia Hoslundiae* Syd.
Hyparrhenia	*Puccinia andropogonicola* Har. & Pat.
	P. erythraeënsis Pazschke
	P. Kaernbachii Arth.
Hypericum	*Uromyces Hyperici* (Spreng.) Curt.
Hypoestes	*Uredo Hypoestis* (Cooke) de Toni
Hypoxis	*Uromyces Hypoxidis* Cooke
Imperata	*Puccinia rufipes* Diet.
Indigofera	*Ravenelia Indogiferae* Tranzsch.
	R. laevioides Arth. & Cummins
	R. maranguensis (P. Henn.) Cummins
	Uredo Indigoferae Doidge
	Uromyces orientalis Syd.
Inula	*Uredo palpigera* Cummins
Ipomoea	*Coleosporium Ipomoeae* (Schw.) Burr.
	Puccinia holosericea Cooke
	Uromyces Ipomoeae Berk.
Jasminum	*Hemileia Hansfordii* Syd.
	Puccinia ugandana Cummins
	Uromyces Hobsoni Vize

Justicia	*Aecidium acanthacearum* Cooke *A. Justiciae* P. Henn.
Kyllinga	? *Uredo Kyllingiae* P. Henn. *U. tesoensis* Wakef. *Uromyces notabilis* Wakef.
Lactuca	*Puccinia minussensis* var. *africana* Cummins
Lantana	*Puccinia natalensis* Diet. & Syd. and var. *Evansii* Doidge
Lathyrus	*Uromyces Pisi* Wint.
Leonotis	*Puccinia leonotidicola* P. Henn.
Leptochloa	*Uromyces Leptochloae* Wakef.
Leucas	*Puccinia Leucadis* Syd.
Lippia	*Aecidium Evansii* P. Henn. *Puccinia lippiicola* Pat. & Har.
Loranthus	*Aecidium Cookeanum* de Toni
Loudetia	*Puccinia Loudetiae* Wakef. & Hansf.
Mariscus	*Puccinia hennopsiana* Doidge
Markhamia	*Uredopeltis congensis* P. Henn.
Medicago	*Uromyces striatus* Schroet.
Melanthera	*Uromyces Melantherae* Cooke
Melinis	*Angiopsora Hansfordii* Cummins *Uredo Melinidis* Kern.
Mentha	*Puccinia Menthae* Pers.
Microchloa	*Uromyces Microchloae* Syd.
Micrococca	*Aecidium Micrococcae* Syd.
Microglossa	*Puccinia aurata* Syd.
Mitracarpum	*Aecidium Mitracarpi* Syd.
Mucuna	*Uromyces Mucunae* Rabenh.
Ocimum	*Puccinia Ocimi* Doidge *Uromyces Ocimi* Hansford
Oldenlandia	*Puccinia Oldenlandiae* P. Henn.
Olyra	*Puccinia deformata* B. & C.
Oxyanthus	*Hemileia Oxyanthi* Cummins
Oxygonum	*Puccinia Polygoni-amphibii* Pers.
Panicum	*Uromyces leptodermus* Syd. *Uromyces linearis* B. & Br.
Paspalum	*Uredo Paspali-scrobiculati* Syd.
Pavetta	*Aecidium flavidum* B. & Br. *Hemileia pavetticola* Maubl. & Roger
Pennisetum	*Phakopsora apoda* (Har. & Pat.) Mains *Puccinia Penniseti* Zimm.
Pentas	*Puccinia pentadicola* Grove *P. Pentadis-carneae* Wakef.
Pergularia	*Uredo Pergulariae* Cummins
Peucedanum	*Aecidium Peucedani-raiblensis* Maire
Phaseolus	*Uromyces Phaseoli* Wint.
Phragmites	*Puccinia Magnusiana* Körn.
Phyllanthus	*Aecidium entebbense* Cummins *A. Phyllanthi* P. Henn. *Uredo Phyllanthi-reticulati* Petch
Polygala	*Uromyces Polygalae* Grove
Polygonum	*Puccinia Polygoni-amphibii* Pers. *Uromyces Polygoni-avicularis* Ramsb.
Prunus	*Puccinia Pruni-spinosae* Pers.
Pseudarthria	*Uromyces Pseudarthriae* Cooke
Psychotria	*Hemileia Holstii* Syd.
Pueraria	*Aecidium Vignae* Cooke
Pycnostachys	*Aecidium Pycnostachydis* (Kalchbr.) Doidge
Rhamnus	*Endophyllum striatosporum* Wakef.
Rhynchelytrum	*Diorchidium Tricholaenae* Syd.
Rhynchosia	*Uromyces Dolichi* Cooke
Ricinus	*Melampsora Ricini* Pass.
Rottboellia	*Puccinia Rottboelliae* Syd.
Rubia	*Puccinia dimorpha* Syd. *P. rubiicola* Syd.

Rubus	*Hamaspora longissima* (Thuem.) Körn.
Rumex	*Uromyces Rumicis* Wint.
Rutidea	*Hemileia Rutideae* Cummins

Scoparia	*Aecidium Scopariae* Wakef. & Hansf.
Secamone	*Hemileia Secamones* Wakef. & Hansf.
	Uromyces Secamones Wakef.
Senecio	*Puccinia Hansfordiana* Cummins
Sesbania	*Uredo Sesbaniae* P. Henn.
Setaria	*Phakopsora apoda* (Har. & Pat.) Mains
	P. elgonensis Wakef.
	P. kigeziensis Wakef. & Hansf.
	P. Setariae-longisetae Wakef. & Hansf.
	Uromyces leptodermus Syd.
Sida	*Puccinia heterospora* B. & C.
Smilax	*Puccinia Kraussiana* Cooke
Solanum	*Aecidium habunguense* P. Henn.
Sonchus	*Puccinia Sonchi* Rob.
Sorghum	*Puccinia purpurea* Cooke
Spermacoce	*Puccinia lateritia* B. & C.
Spilanthes	*Puccinia africana* Cooke
Sporobolus	*Puccinia kakamarensis* Wakef. & Hansf.
	Uromyces tenuicutis McAlp.
Stizolobium	*Uromyces Mucunae* Rabenh.
Strophanthus	*Hemileia Buntingii* Wakef. & Hansf.
	H. Smallii Wakef. & Hansf.
	H. Strophanthi Rac.
Stylosanthes	*Uredo Stylosanthes* P. Henn.

Teclea	*Puccinia Tecleae* Pass.
Themeda	*Puccinia versicolor* Diet. & Holw.
	Uredo Anthistiriae-Tremulae Petch
	U. themedicola Cummins
Thunbergia	*Puccinia Thunbergiae-alatae* P. Henn.
Toddalia	*Ctenoderma Toddaliae* (Petch) Syd.
	Puccinia Tecleae Pass.
Tragia	*Puccinia Tragiae* Cooke
Tragus	*Uromyces Tragi* Wakef. & Hansf.
Tricholaena	See *Rhynchelytrum*
Trichopteryx	See *Loudetia*
Trifolium	*Uromyces elegans* (B. & C.) Lagerh.
Tristemma	*Puccinia necopina* Grove
Triticum	*Puccinia glumarum* (Schum.) Eriks. & Henn.
	Puccinia graminis Pers.
	Puccinia triticina Eriks.

Urochloa	*Uromyces leptodermus* Syd.

Vangueria	*Aecidium Vangueriae* Cooke
Vernonia	*Aecidium Vanderystianum* P. Henn.
	A. Vernoniae-podocomae Doidge
	Melampsora Junodii Doidge
	Puccinia Hansfordii Wakef.
	P. Le Testui Maubl.
	P. vernoniicola P. Henn.
	Uredo perscita Cummins
Vicia	*Uromyces Fabae* (Pers.) de Bary
Vigna	*Aecidium Vignae* Cooke
	Uromyces Phaseoli Wint.
Vitis	*Uredo cissicola* Cummins
Vitex	*Olivea scitula* Syd.

Wedelia	*Puccinia kampalensis* Cummins

Zea	*Puccinia Sorghi* Schw.
Zornia	*Puccinia Zorniae* McAlp.

GOETHE'S INTEREST IN BRITISH BOTANY

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Goethe, the bi-centenary of whose birth will be commemorated this year, stated in a survey of his botanical studies : ' Not only in my country, but also abroad, I am known as a poet and even recognised as such ; my intensive study of nature and its general and organic phenomena, my conscientious observations, pursued passionately, though quietly, have found but little attention '.

In the scholarly edition of Goethe's works, the scientific writings occupy 13 out of a total of 66 volumes. From Goethe's diaries, letters and conversations (another 70 volumes), it appears that for many years, scientific studies occupied him more than did his duties as State-minister or his literary works. Of his scientific works, only the *Theory of Colours* and the *Metamorphosis of Plants* have been translated into English [the latter by Emily M. Cox in the first volume of *Journal of Botany* and separately (1863), and again in recent years by W. T. Stearn in *Notes and Correspondence of the Anthroposophical Agricultural Foundation*, **4**, no. 8 (April 1937) and by Agnes Arber in her paper on ' Goethe's botany ' in *Chronica Botanica*, **10**, no. 2 (1946), pp. 91–120]. The historical sections of Goethe's optical and botanical works have never been translated, and even in many German editions (including the Jubilee-edition) they were not considered worth re-printing in full ; the detailed knowledge which Goethe displayed in his scientific studies of the eminent contributions made to these fields by Great Britain, has never been appreciated.

In the history of science and of studies on Goethe, Goethe's scientific works have fallen between two chairs. In the light of 150 years of scientific progress they appear as obsolete ; amateurish as they are, they fall short even of the standards of science at his time. Their influence, due to the weight of Goethe's name, appears as mere obstruction. With regard to Goethe's botanical studies, Julius Sachs established this opinion in so authoritative a manner that later historians of botany, such as Professor Harvey Gibson, saw no reason to re-examine it from the sources or from a more advanced historical point of view. On the other hand, literary students, notably those who took an interest in Goethe's knowledge of English literature (such as Karl Sachs in 1905 or James Boyd in 1931) avoided his scientific works, apparently because, in the light of such expert criticism, they felt incompetent to deal with them in detail. The attempts, to this day occasionally made, to save Goethe's scientific theories, such as metamorphosis of plants, are a source of amusement to the scientist and of embarrassment to the literary student.

The study of Goethe's botanical works as a source of his knowledge of the British contribution to this field of learning may revive, in some small measure, both scientific and literary interest in these works.

At the end of his *Metamorphosis of Plants* (1790), Goethe said : ' If the contents of these pages appear as superfluous, they should be considered in the historical perspective as the record of quiet, steady and consistent activity '. The quietness of Goethe's botanical studies can be illustrated through a survey of their British associations. Though Goethe admitted that a Briton was the greatest botanist of his age, though in both the practical and the literary field he showed a wide acquaintance with British botany, and though he went so far as to translate most carefully an English botanical text, these associations have never been noted by students of his botanical works. The steadiness of his botanical pursuits also showed itself in his British associations, which extend from the very beginning of his interest in this field right to the end of his life. However, it is above all the third of the three qualities claimed by Goethe for his botanical studies, which is displayed in his British associations. Although no British scientist held a central position in these studies as Newton occupied in Goethe's physical studies, Howard in his meteorological investigations, or even Hunter in his physiological, or Mawe and Macculloch in their mineralogical works, these British associations were an important point in his system, illustrating the extent and conscientiousness of his studies and finally confirming him in his theoretical beliefs.

In no sphere of his scientific activities has Goethe been more severely criticized by specialists than in his botanical studies. It should be remembered that botany was the first scientific field to which Goethe devoted his attention. To this more than to any other sphere of his pursuits applies what he wrote at the time when his interest in botany took shape (during his journey through Italy). ' Oh, that I had had a wise Englishman for my father, that I need not acquire everything and conquer everything for myself ! ' Scott, at hearing from his son-in-law, on his return from Weimar in 1817, that Goethe was interested in botany, is said to have exclaimed : ' I am glad that my old master has interests akin to mine '. On 3 February 1823, Scott signed the diploma of membership of the Royal Society of Edinburgh, which Schwaegrichen, the botanist at Leipzig, obtained for Goethe. Goethe's position as a scientist (though mainly in the mineralogical field) was acknowledged by similar diplomas from the academies of New York, Dublin and St. Petersburg.

In one of his conversations with Eckermann on the subject of English literature (24/2 and 18/5 1824) Goethe admitted that he had recognized that botany had become too highly specialized to admit amateurish activities.

The only scientists referred to in his *Metamorphosis of Plants* are Linnaeus, ' my great master ', Ferber, also a Swede (better known in this country as a mineralogist, by his *Oryctography of Derbyshire*, 1776), Gaertner, one of the most advanced German followers of de Jussieu's idea of a natural system, Batsch, the botanist at Jena, and Hedwig, a friend of Schwaegrichen. In the survey of his botanical studies, embodied in the essay on *Formation and Transformation in organic Nature*, Goethe paid an even greater tribute to Linnaeus, saying that apart from Shakespeare and Spinoza, he exercised the greatest influence on him. In 1809 (28/2) he had told a friend that his theory of the metamorphosis of plants had now been so generally adopted, without acknowledgment to its initiator, as had Bacon's discoveries, a remark which led Goethe to a lengthy exposition of the foundations of scientific development in late mediaeval England.

The earliest document of Goethe's systematic interest in botany is the letter which he wrote to his friend Knebel from Italy (3/10/1787) : ' I am studying botany everywhere. It may sound presumptuous when I say that I believe I have well advanced in these studies. However, I have become more and more confident that I have found a general formula applicable to all plants. I only want time for developing this idea. Italy is an ideal ground for such studies ' ; Goethe devoted special attention to the botanical gardens there. Referring to a ' carnation, from which four other different carnations had grown ', Goethe added : ' This phenomenon is quite different from that described by Hill, who published a small treatise on such plants '. This is a memory of Goethe's earlier reading, during a visit to Loder, the anatomist at Jena, of ' Hill's treatise on flowers growing new flowers from their centre ', referred to in his letter to Frau v. Stein of 12/12/85, and followed by the significant remark : ' If I had only a special gift for the sciences ! ' Through the German translation (Nuremberg 1776) of John Hill's book on the *Origin and production of proliferous flowers* (London 1759), Goethe became first acquainted with that phenomenon which was to become the starting-point of his *Metamorphosis of Plants* (paragraphs 1, 2 and 105). There is no record of Goethe's reading

Hill's earlier explanation of the Linnaean system or his letter to Linnaeus on the *Motion of sensitive plants* (1761) which would have been of interest to his studies in the spiral tendency of plant movements.

Many of Goethe's early associations with British science are derived from his extensive reading of books by and on British scientific travellers, a subject of which we have recently learnt more through a survey of works borrowed by him from the Weimar library. To mention but one example of interest to his early botanical studies, as early as 1774, he referred, in a poem (*Sendschreiben*), to Sir Joseph Banks's travels ; the name of Banks became so familiar to him that in 1797 he confused Sir Joseph with Joseph Blank, O.F.M., professor of natural philosophy at Wuerzburg (Weimar-edition, series I, vol. xxxiv, 1, p. 324, and series III, vol. ii, p. 130). During his journey through Italy, Goethe noted from Richard Payne Knight's *Expedition to Sicily in* 1777, that ' vine, figs and mulberry trees are raised in England in hot-houses and with special care '.

At that early stage of his studies, Goethe did not hesitate to derive scientific information even from such works as Erasmus Darwin's *The Botanic Garden*. Reviewing the contents of that work, in a letter to Schiller (25/1/1798), he noted that it also dealt with botany, namely in canto iv of the first book, which had extensive notes on vegetable perspiration, placentation, circulation and glandulation, and especially the second book, entitled *The Loves of the Plants*, starting with an exposition of the Linnaean system, carrying numerous beautiful illustrations of the plants referred to, and concluding with an index of more than 100 plants.

Through his interest in agriculture and horticulture, in particular in botanical gardens and parks, Goethe obtained much of his early information on the practical aspects of British botany. Among Goethe's associations with British agriculture, the most striking is his friendship with George Batty, who, in the late 'seventies of the 18th century, entered the Weimar state service to introduce modern irrigation of meadows. Goethe had the highest opinion of Batty's character and work. He frequently discussed with him ' details of agriculture '. When native ' experts ' tried to delay the improvements proposed by Batty, Goethe supported him most energetically. In 1780 he stated that in his official work he trusted no one as much as Batty. Right to his death in 1820, Batty had in Goethe a faithful friend. A still more explicit tribute to the superiority of British agriculture is found in Goethe's poem on Thaer's 73rd birthday, in which Goethe referred to the decisive influence exercised upon this great agronomist by the study of intensive cultivation as practised in Britain. In spring 1824 Goethe had borrowed from the Weimar Library Thaer's *Introduction into English agriculture* (Hanover 1798). In contrast to this method, the then state of agriculture in Germany appeared to Goethe as ' *Schlendrian* ' (in his dealings with Batty he even spoke of ' *Sauerey* '). He spoke on this subject to Zelter, who was to set his poem on Thaer to music (letter 11/3/24). In another letter to Zelter (5/10/1828), Goethe drew on information obtained through his meteorological studies when referring to ' the moist storms sweeping, from the Western ocean, over England, where this year agriculture has been greatly injured by excessive rainfall '. In 1808, in a letter to Bettina von Arnim (22/6), he had spoken of the ' lovely green lawns of England due to mist and fog '—a subject referred to in every German travel book on England. These are typical examples of the connection of Goethe's interests with his studies in other spheres.

In 1807 (diary 4/11) Goethe learnt (from a source not stated by him) of the ' amusing experiment of an Englishman who grew beans on a continuously revolving wheel in order to observe where the roots or rootlets (*Federchen*) would grow. The roots are said to have grown outwards, the rootlets inwards '. Another example of Goethe's interest in botanical experiments is found in a literary essay written in 1816, where he speaks of the good example given by English horticulturists in associating for the cultivation of certain species, e.g., gooseberries, ' each associate undertaking to grow one particular variety with special care ' (Weimar-edition I, xxxiv, 1, 126 f). Through his intensive study of the history of the Royal Society in his history of optics, Goethe had formed the opinion that England was the ideal country of scientific organization.

While the development of Goethe's studies in physics, meteorology and mineralogy cannot be thought of without his associations with British science, the active phase of his botanical studies shows but little definite evidence of such associations. It was only after the end of the Napoleonic wars that he became systematically acquainted with English scientific literature in the botanical field. In October 1815, complaining to his friend Boisserée at ' the mad luxury carried on in England with regard to books ', Goethe mentioned as an example ' a botanical work exclusively treating of pine trees, costing 80 guineas '. This may be a reference to Aylmer Bourke Lambert's *Description of the genus Pinus* (London 1803), two folio volumes, which Goethe borrowed in 1826 from the Weimar Library. In 1818 Goethe read *The Exotic Gardener* (London 1814) by J. Cushing, ' foreman to Messrs. Lewis & Kennedy at Hammersmith ' ; in the German translation by G. F. Seidel (Dresden 1817) the sub-title of this work was rendered by ' The method by which the English treat and propagate plants in hot-houses '. Cushing's work was dedicated to Banks and contained an index of all the species known to be cultivated in hot-houses in Britain.

A few months earlier (12/12/1817), Goethe had read in an unspecified ' English journal on a special method of planting oak-trees '. This may have been one of the numerous general magazines to which, one may say, the Weimar aristocracy then became addicted. From 1816, we can trace a series of references made by Goethe to his systematic reading of *Curtis's Botanical Magazine* and other British botanical periodicals. As early as 4 January 1793 though, Goethe had noted, among references to German scientific works, ' Bot. Mag.', which (as there was no *Botanisches Magazin*) can only be Curtis's magazine.

In his botanical studies, as in his meteorological and mineralogical ones, Goethe owed many decisive impulses and British associations to his patron, the Grand-Duke of Weimar. In his plan of an essay on the cultivation of plants in the Grand-Duchy, Goethe remarked that on his journeys through France and England (in 1816), the Grand-Duke had made a special study of the botanical gardens and other scientific establishments. Goethe urged the Grand-Duke to publish a summary of his observations on this subject for the benefit of German scientists, and as an indication of the Grand-Duke's qualifications in this sphere, he mentioned that he was ' the first honorary member of the Horticultural Society of London '. By order of the Grand Duke, the botanical gardens at Weimar regularly obtained seeds and plants from England. In September 1820 Goethe acknowledged to his secretary the arrival of a parcel (probably of seeds) from the ' English Horticultural Society ' for the Grand-Duke, which, he said, was not to be opened until the Grand-Duke had returned from his holiday. In the same letter, Goethe asked his secretary to obtain for him (from the library) ' that part of Curtis, one of the late ones, which contained an illustrated description of *Bryophyllum calcycinum?* This special item had been referred to by Goethe, in his diary for 30 December 1818, with its exact location, namely, ' Curtis *Botanical Magazine*, vol. 34, pl. 1409 ', which had appeared in 1811, but apparently did not reach Weimar until the end of the war. When we consider the variety of subjects with which Goethe had dealt during the subsequent two years, we may realize how seriously he took his botanical studies to remember this item and its approximate location. In 1828 (diary 29/12) Goethe perused the *Botanical*

Magazine for a reference to *Ferula* (no. 2096 in vol. 46, 1818), and in 1830 (diary 29/10) he recorded the arrival of the first volumes of the new series of this magazine (that is, of course, the second 'new series'—beginning with vol. liv in 1827—not the first one, which began with vol. xliii in 1816). From the records of the Weimar Library it appears that Goethe borrowed of *Curtis's Botanical Magazine*, vols. 35–42 from 17/6 to 12/8/1821 (together with Sir Richard Colt Hoare's *Ancient History of South Wiltshire*, 1812), 33 and 34 from 30/12/1818 to 2/1/1819, 31 from 19/1 to 5/2/1819, 35 and 36 from 5/2 to 3/3/1819, 33 and 34 again from 6/9 to 27/10/1820, and vols. 1, 2, 7, 8, 17, 18, 45 and 46 from 5 to 7/11/22 (together with Conrad Loddiges, *The botanical cabinet, consisting of coloured delineations*, the plates being by George Cook, vol. 1–3, London 1816–1822, and John Lindley—see below—*Collectanea Botanica*, London 1821). From 1 to 3/5/1823 and on 31/1/1825 Goethe borrowed the Index volume of Curtis, then again vols. 17 and 18 from 7 to 24/1/1827, vol. 46 from 30/12/1828 to 6/1/1829, vols. 9, 10, 21 and 28 to 31 to 40 on 2/12/1830 (together with *Botanical Register*, vol. 7), and vols. 44 and 51 and 'N.S. 1.2' (together with *Botanical Register*, vol. 3 and 4.2, and various botanical works in French and German) 29/10/1830, apparently not returned until after Goethe's death.

Goethe gave us interesting information on the spreading at his time of concrete botanical information from England. In 1825 (letter 3/11) he identified a plant submitted to him as *Zizania palustris* L. 'a variety of grass used either for decorative purposes, or, in North America, for practical purposes. It deserves the attention of botanists. Sir Banks [!] introduced it from Canada into English gardens ; an excellent illustration of it was given by Franz Bauer in *Linn. Transact.* vii' (1804, p. 264 f., in a paper on *Zizania aquatica* by Aylmer Bourke Lambert—see above. On 6 September 1820, Goethe had sent to the Grand Duke '6 Bände von der Linneischen Societät', specified as 'Acta der Linneischen Societät', that is, the Linnean Society of London; Goethe stated that Hüttner, the book-agent of the Weimer Court at London, had procured these volumes for him 'with considerable difficulty'. From 30/9 to 4/10/1823 Goethe had borrowed from the Weimar Library vol. 4 (1798) of the *Transactions of the Linnean Society*. Other illustrated works of British botany read by Goethe are John B. Ker's *Icones plantarum sponte in China nascentium* (diary 23/3/1821) and Elizabeth Blackwell's *Herbarium Blackwellianum*, prefaced by Trew and illustrated by Eisenberger (Nuremberg 1757–1759, borrowed from the Weimar Library in April 1828), also Nicolaus Joseph Jacquin, *Plantarum rariorum horti Caesarei Schoenbrunnensis descriptiones et icones* (Viennae 1797 to 1804, borrowed from the Weimar Library in August 1825).

In his letter of 3 November 1825 Goethe continued : 'A seed of this plant was brought, by Professor Treviranus, in water from England to Breslau, where it was successfully grown in large quantities in the botanic gardens'. (In his article on Treviranus, in *Allgemeine Deutsche Biographie*, Wuenschmann referred to Treviranus's holiday tours through England and Scotland ; in 1829, Treviranus exchanged, for political reasons, his professorship in Breslau with Ness von Esenbeck in Bonn, of whom more presently). It would appear that Treviranus sent a sample of Breslau-grown *Zizania palustris* to the Weimar Botanic Gardens. Writing in 1830 (Weimar ed. I, xliii, 1, p. 42) on the catalogue of the botanic gardens at Prague, Goethe stated that they had 'none of the new fancy plants propagated from England', but in 1831 (diary 1/5) he admired in the Weimar botanic gardens 'gorgeous primula auricula, especially the English varieties' (described in Curtis only in vol. cxi, 1865).

In 1827 (44) Goethe received from Nees von Esenbeck, in a collection of seeds, a species described as 'Arrarut', which he identified from Oken's manual of botany as the German phonetic spelling of 'Arrow-root' (in German, literally translated by '*Pfeilwurz*'), which he supposed to be related to *Maranta indica.*

He asked Nees von Esenbeck to write to 'Herr Sabine [Joseph Sabine, secretary of the Horticultural Society] in London for seeds of *Mango* as described in the latest issue of the Journal der *Royal Society*' (I was unable to identify this reference). Goethe suggested that some of these seeds should be sent to Poppelsdorf, the botanic gardens of Bonn, of which Nees v. Esenbeck was the director and his brother the inspector, and a few to himself. These seeds, Goethe said, could be procured from England, 'because this plant ripens in England'.

Nees von Esenbeck was among the most eminent of Goethe's botanical friends (see Wuenschmann's article on him, *l. c.*), and it was to him that Goethe owed his acquaintance with the works of Robert Brown. The name of Robert Brown occurs for the first time in Goethe's works, in his diary for 28 November 1820, in an entry relating to his reading of Nees von Esenbeck's *Botanical Dictionary*. The words 'Botanische Beobachtungen von Robert Brown über die Syngenesisten' refer to Brown's essay on *Compositae* in *Trans. Linn. Soc.* **12** (1816), pp. 76–142. In his Annals for 1820, reviewing his major activities during that year, Goethe said that Brown's remarks on this subject were 'considered in detail, studies in the Jena botanic gardens affording facilities for doing so'. Robert Brown was born in 1771, Nees von Esenbeck in 1776; both died in 1858.

On 10 January 1825, Goethe wrote to Nees von Esenbeck: 'I am greatly looking forward to Brown's works and to what you will tell us about him; I can hardly await an opportunity to form a clearer opinion of this excellent man'. Later in the year appeared at Schmalkalden the first volume of the German translation of Brown's *Miscellaneous Works,* containing his essays on plant geography. Nees von Esenbeck seems to have planned this translation as far back as 1820, and from the outset he enlisted Goethe among its supporters. In Goethe's diary for 28/11/1820, the reference to Brown's essay is followed by the words 'Translation, manuscript'. Nees von Esenbeck's preface to the first volume of the translation of Brown's works pays a singular tribute to Goethe's work as a botanist, at the same time acknowledging the indebtedness of German botanists to Brown. As this translation is now not easily accessible, a translation of the relevant passage from Nees von Esenbeck's preface may be acceptable.

> 'Following Jussieu and keeping pace with von Humboldt, Robert Brown, always based on his own judgement and observations, has endeavoured in most of his writings to develop the natural system of plants in the most specialized manner, by thorough experience. He has not been contented with compiling the results of his studies, but has permitted us to see the ways in which they have been obtained, informing us always of the stages of his investigations, doubts he had to remove and observations he had to clarify. Thus, the principle found in the end becomes our own. This method is exemplary for all similar undertakings, because it supplies illustrations of thorough investigation on the natural system, and these illustrations are sufficient in size and difficulty to prevent mistakes. I recommend this master in particular to our younger generation. [Brown initiated plant geography.] Since 1810 he has devoted himself to the investigation of the natural relationship of plants. What attracts us most to him is the idea of metamorphosis, always transparent through the most faithful pursuit of his object. This idea is the principle of his family groups. From the observation of the variety of data, he attains to a vision not only of the existing similarities and differences, but also of the reasons of this connection and the possibility of all other forms, which may originate from such a circle of related specimens, without breaking it, but either opening a new circle—hitherto unknown—or transcending into

> an adjoining one, previously known. In this respect, our author is most brilliant and comparable to Goethe, at the same time however his antipode, without infringement of the honour due to either of them. What was pronounced by Goethe and gathered into one great idea for the plant world, as an echo of the first word of creation, was expressed everywhere by Robert Brown through his abundant experience, full of observations, rich in comparisons, straight from the silent mouth of the individual plant. Recognizing the plant world as a whole, he sought for himself and for others the one significant and binding term, word and character for each species and family. He often spoke prophetically of plant families still to be discovered.'

In his survey, published in 1831, of the influence exercised by his work on the metamorphosis of plants upon botanical studies of the last forty years, Goethe stated that among those who assigned metamorphosis a certain place in their system,

> ' we may also boast of a name of significance, that of Robert Brown. It is characteristic of this great man not to talk much of the fundamental truths of that branch of science cultivated by him, and yet to show in each of his books that he is intimately aware of them. Therefore the complaints of the lack of clearness in his writings. He has never dealt extensively with metamorphosis. Only once, in a note to his essay on *Rafflesia*, when saying that he regarded all parts of blossoms as modified leaves, he tried to explain the normal formation of the anther in accordance with this theory. Made by him who is recognized to be the greatest botanist of our age, this casual remark has not failed to exercise influence, especially in France. In particular Aubert du Petit-Thouars, who is praised by Brown as one of the important advocates of this theory, seems to be indebted to Brown's high opinion, for the esteem to which he has now attained in France.'

Brown's essay on *Rafflesia* was published in the *Transactions of the Linnean Society*, **13** (1820), pp. 201 to 234, and it appears that the reference to it in Goethe's essay was based on the original rather than on the translation published in Oken's *Isis* (October 1823, pp. 1356 to 1384) or that (by Dr. Pauls in Coblenz) which appeared in the second volume of Nees von Esenbeck's edition, (Leipzig 1826). Goethe's essay was a collection of reviews of or references more or less direct, to his *Metamorphosis of Plants*. Many of these references were supplied to him by his friends, and such passages, Goethe said, were marked by brackets or asterisks. The passage on Brown was not marked in this manner, although it occurs verbatim in a letter which, on 8 April 1823, had been addressed to him by Ernst Meyer, the botanist in Goettingen, who was to become one of the co-editors of Nees von Esenbeck's German edition of Robert Brown's works (see *Goethe-Jahrbuch*, v, 151). In his essay *Reply* (on the subject of metamorphosis, dated 17 March 1823, but not published until 1831), Goethe had stated that like Ernst Meyer, he recognized

> with admiration in the works of de Jussieu and Robert Brown how these men, trusting their genius, had been able to work as if, whatever we are missing [in their works], had been at their disposal long ago. We then conceive no hope that among us there will arise men equal or even superior to them. We will never be persuaded to despise these men only because they are foreigners.

Considering these significant statements of Goethe's attitude to foreign scientists and to the history of science, we must remember that Goethe was Brown's senior by twenty-two years.

In 1826, Meyer, through Goethe's influence, was appointed professor of botany at Koenigsberg ; he was the first to write a history of botany and his plan to bring this work up to Robert Brown was a singular tribute to the high esteem in which he too held that British botanist. Of the German edition of Brown's works, Goethe may have seen the first four volumes (the third, published in 1827, was *Prodromus Florae Novae Hollandiae*) ; the fifth volume appeared two years after his death. It seems that this German collection inspired the publication in 1866 of *The Miscellaneous Works* of Robert Brown in this country.

Further in his essay on the effect of his *Metamorphosis of Plants*, Goethe reviewed a note from *Botanische Literatur-Blaetter*, ii, 3 (Nuremberg 1829), p. 427—a periodical apparently not available in this country—saying that 'in the Royal Institution of Great Britain at London on 30 January 1829, Herr Gilbert T. Burnett read a long paper on the metamorphosis of plants. This is here translated in extracts, and it would be desirable to see the whole. It does not seem to be in complete agreement with our ideas, but to treat of the matter in a serious and intelligent manner'. In vol. i of the *Journal of the Royal Institution of Great Britain* of October 1830 appeared a paper ' On the development of the several organic systems of vegetables with reference to their function ' by Gilbert T. Burnett, who in 1835, the year of his death, was to publish a book on a natural system of botany. The report in the Nuremberg magazine therefore was based on private intelligence. There is no evidence of Goethe's wish to see the whole paper being fulfilled ; in the *Journal of the Royal Institution* Burnett's paper was followed by a review of Purkinje's *Optics*, in which Goethe is mentioned, a foot-note saying that ' an account of the *Farbenlehre* of this illustrious poet and philosopher will follow ', a promise which was not kept.

It was probably in connection with the translation of Brown's essays that Goethe became interested in English botanical terminology. In 1824 he remarked that ' to the honour of botany it must be admitted that its terminology becomes more and more flexible and refined ; just at the present moment, curious examples of this development have become known through the last few issues of Curti's (!) botanical magazine ' (Weimar-edition ii, vol. vi, 177 f.). There is more explicit evidence of Goethe's interest in this matter.

His last botanical work, published in 1831, was devoted to the spiral tendency of plant motion. Among the paralipomena to that work, a note has been preserved saying : ' David Don of Edinburgh, phenomenon of noticeable motion. Duglas (!) recognized the spiral turning of whole plants '. (Weimar edition II, vii, p. 363 f.) David Douglas (to whom Lindley dedicated the genus *Douglasia*) was a fellow of the Linnean Society and contributed to its *Transactions* ; David Don succeeded Robert Brown as librarian to the Linnean Society, he was also a friend of Alexander von Humboldt, who of course was intimately acquainted with Goethe. In 1829 (2/4 diary) Goethe had read ' in a new issue of the Edinburgh magazine a short note on the presence of spiral vessels in all parts of plants '. This note, which confirmed Goethe in the theory then expounded by him, was subsequently translated by him for his essay on the spiral tendency of plant motion, where it appeared under the title ' Edinburgh new philosophical Journal October–December 1828 (Seite 21) ' (Weimar-ed. II, vii, 43 f.) In preparing translations of English scientific texts (as he also did in his studies on optics, meteorology and mineralogy), Goethe proceeded most carefully. Exactly two years after reading Don's note, he entered in his diary : ' In the evening, Professor Riemer. We corrected the translation of the spiral vessels with reference to the original '.

The most striking feature in Goethe's translation of Don's note is the relationship between the English words ' style, stem, stalk ' and the German words ' Stiel, Griffel, Stengel, Stamm '. ' Style ', for instance, is rendered with regard to *Scabiosa atro-purpurea* by ' Griffel ', with regard to *Nigella hispanica* by ' Stiel ', ' stem ' with regard to *Urtica nivea* by ' Stamm ', with regard to

Polemoniacaeae by 'Stengel'. Another significant feature, common to Goethe's scientific translations, is the tendency to use German terms even where the German scientist would be inclined to use the Latin term; thus he has for, 'plexus' 'Geflecht', for 'transversal fracture' 'Querbruch', for 'segment' 'Abschnitt' and for 'fibre' 'Faser'. The carefulness of Goethe's translation may be seen from the fact that in some instances he inserted the English word in brackets after his tentative German translation (e.g. 'Höhlung (*pith*)') or offered two alternative German expressions for an English word (e.g. 'pieces of bark' rendered by 'Teil/Stückchen der Rinde'). This translation should be related back to Goethe's first botanical work, in the introduction to which he discussed the meaning of '*Stengel* or *Stamm* or whatever takes its place' and of '*Rinde* (bark), *Haut* (skin) or *Schale* (shell or peel)'. His translation of Don's note illustrates not only the development of his English scientific vocabulary but also that of his German botanical terminology, an important chapter in the history of botany.

In his note, Don referred to an article by John 'Lindley in the last issue of Botanical Register'. Though it appears that Goethe did not actually see Lindley's essay we may list Lindley (then professor of botany in the University of London) as the seventh British botanist referred to by Goethe. Casual and indirect though some of these references were, they contribute towards our knowledge of the history of British botany, its organization and in particuar its influence abroad.

As a foot-note to this survey I wish to draw attention to Goethe's reading of a British work on paleontology. In 1826 he read E. T. Artis's *Antediluvian Phytology, illustrated by a collection of the fossil remains of plants peculiar to the coal formations of Great Britain* (London 1825), in the preface to which special tribute is paid to two friends of Goethe's, Count von Sternberg and Noehden. Through this work, the British associations in Goethe's botanical studies are linked up with those in his mineralogical studies, a subject which I have surveyed elsewhere.

Summary : From 1776 a series of references to British botany can be traced in Goethe's works, but it was only after the conclusion of the active phase of his botanical studies that Goethe became fully aware of scientific botany in Britain. He read British botanical publications extensively. He recognized Brown as the greatest botanist of his age and took a lively interest in the German edition of his works. He also referred to Banks, Burnett, Don, Douglas, Hill and Lindley. His translation of a short essay by Don is an important record of the development of his botanical terminology.

Sources : None of the works on Goethe as a botanist has referred to the British associations in his studies. In general, Goethe's knowledge of British science has never been investigated. References to Goethe's works have been translated from the Weimar-edition, and their location has been stated only where it cannot be traced without difficulty from the excellent indexes (the index to Goethe's botanical works was compiled by the editor of this section in the Weimar-edition, Rudolf Steiner, the founder of anthroposophy).

PROCEEDINGS OF THE ANNIVERSARY MEETING
24 May 1949

Professor G. R. DE BEER, F.R.S., President,
in the Chair.

The Proceedings of the General Meeting held on Thursday, 12 May 1949, having been circulated, were taken as read and confirmed.

The President welcomed the presence at the meeting of Dr. E. M. Bircher, Secretary of the Swiss Legation, and Professor Maurice Caullery, F.M.R.S., F.M.L.S.

The sending of a telegram congratulating Mr. William Stone, M.A., on his completion of seventy years as a Fellow of the Society was reported by the President :—

> 'Linnean Society of London in Anniversary Meeting assembled sends you congratulations and best wishes on seventieth anniversary of your election into the Fellowship'.

The following Fellows signed the Obligation in the Roll and Charter Book, and were admitted Fellows :—Professor John Leslie Audus, M.A., Ph.D., Mr. Guy Oldfield Allen, M.A., Mr. Arthur Paul Benthall, Miss Frances Ethel Ince, M.Sc., Dr. Betty Louise Moss, M.Sc., Miss Margaret Naylor, M.Sc., Mr. Mark Ogilvie-Grant, B.A., Dr. Francis Ralph Tubbs, M.Sc., Dr. Lille Ethel Wagge, B.Sc., Mr. Alan Douglas Whitehead, B.Sc., and Mr. John Frederick Woolman.

Candidates for Fellowship were balloted for and elected :—Professor Arthur Roy Clapham, M.A., Ph.D., and Leslie Francis Seawell Ward, M.A.

Dr. David Fairchild, of Coconut Grove, Florida, U.S.A., was balloted for and elected a Foreign Member.

The Bye-Laws regulating the Election of Council and Officers having been read by the Assistant Secretary, the PRESIDENT declared the Ballot for new Members of Council to be open, and voting began. The PRESIDENT thereafter appointed Mr. I. H. BURKILL, Mr. A. E. ELLIS and Mr. R. WINCKWORTH, as Scrutineers of the Ballot.

The Ballot was closed at the due time, and the result declared to the Meeting,—NEW MEMBERS OF COUNCIL.—Prof. A. J. E. Cave, M.D., D.Sc., Dr. E. B. Ford, M.A., F.R.S., Prof. F. E. Fritsch, D.Sc., Ph.D., F.R.S., Mr. C. C. Hentschel, M.Sc., and Dr. C. F. A. Pantin, F.R.S.

(The retiring Councillors were Mr. A. H. G. Alston, Prof. G. R. de Beer, F.R.S., Mr. James M. Fisher, Dr. Edward Hindle, F.R.S., and Dr. Malcolm A. Smith.)

The PRESIDENT declared the Ballot for Officers to be open and voting began. The Ballot was closed at the due time, and the result declared to the Meeting,—OFFICERS.—*President* : Professor F. E. Fritsch, F.R.S. ; *Treasurer* : Colonel F. C. Stern, O.B.E., M.C. ; *Botanical Secretary* : Dr. B. Barnes ; *Zoological Secretary* : Dr. A. Tindell Hopwood.

The President then called upon Professor DAVID MEREDITH SEARES WATSON, F.R.S., Professor FREDERICK ERNEST WEISS, F.R.S., F.L.S., and Dr. WILLIAM THOMAS CALMAN, C.B., F.R.S., F.L.S., who had been selected as recipients of the Linnean Medal, and after addressing them in turn, presented them with the Medals.

In handing the Linnean Medals to the recipients, the PRESIDENT spoke as follows :—

Professor David Meredith Seares Watson

In awarding you the Linnean Medal for 1949, the Linnean Society is proud of the opportunity of adding your name to the list which already contains those of Richard Owen, Thomas Henry Huxley, Ray Lankester, E. S. Goodrich and Maurice Caullery. In your researches into the comparative anatomy and palaeontology of vertebrate animals, you have probably contributed more objective evidence than anyone in this country to the unravelling of the problems of the evolution of the most important groups of these organisms. I need only mention your work on the origin of the Amphibia, of the palaeoniscid fishes, of the acanthodian fishes, and of the frogs, as examples. I am also mindful of your masterly demonstration that the Pterodactyls were warm-blooded animals. All the Fellows of the Society are deeply grateful to you for the Hooker Lecture which you delivered last year. At the same time, your interest in all the wider aspects of zoological science has made of you our acknowledged leader in this field : a fact that is reflected in your membership of no less than five National Academies of Science. It is therefore with the greatest pleasure that I hand to you the Linnean Medal.

Professor Frederick Ernest Weiss

In awarding you a Linnean Medal in respect of the War years, the Society is acquitting itself of a heavy debt to an old friend. It is sixty one years since you were elected a Fellow of this Society, and I am both sorry and glad to tell you that you are nevertheless not its Father ; I am confident that you and the Society will approve the telegram which I have this day sent to Mr. William Stone.

You have served repeatedly on the Council of this Society ; you have been very generous in presenting to our library a number of valuable and rare books and publications, and you have occupied the Presidential Chair from 1931 to 1934 ; no one can turn to the Proceedings for those years without being struck and charmed by your Addresses, on the Stigmarian Problem, the Extension of the Mediterranean Flora, and the Phenomenon of Variegated Foliage. We are also mindful of your contributions to palaeontology, the biology of flowering plants, plant ecology, and of your interest in gardening. We are also glad to remember, that as a good Fellow of the Linnean Society, your interests have always embraced the whole of biology, and that among your earliest publications were papers on cuttle-fishes and on Amphioxus. In adding your name to the list of recipients of our medal, in succession to Hooker, de Candolle, Strasburger and Scott, the Society honours itself.

The President read the following telegram : 'The President, Linnean Society. Please convey to Professor Weiss congratulations of Botany Department Manchester. Ashby '.

Dr. William Thomas Calman

In awarding you a Linnean Medal in respect of the War years, the Society is likewise acknowledging its debt to and esteem for an old friend. In addition to long periods of service on the Council, you have been Zoological Secretary, and President. Your Addresses on the Meaning of Biological Classification, the Origin of Insects, and on James Eights, a pioneer Antarctic Naturalist, reflect the width and the depth of your interests and contributions to zoology. Your text-book on the Crustacea has earned you a lasting place in the curriculum and on the shelves of all students. During the long period when you were Keeper of Zoology at the British Museum (Natural History), you brought unbounded credit to this Society. In handing you this medal I hope that you will allow me to say what you once said to me when I first joined this Society : 'lang may your lum reek '.

The President presented the diploma of Foreign Membership in favour of Professor Dr. Otto Jaag to Dr. E. M. Bircher, Secretary of the Swiss Legation, for transmission to Zurich.

The Librarian and Assistant Secretary presented his Report.

LIBRARIAN AND ASSISTANT SECRETARY'S REPORT

List of the Society.—Since the last Anniversary Meeting the Society has lost 30 members. The detailed statement is as follows :—

18 *Fellows by death.*—E. P. Allis, junr., J. H. Bell, W. Borlase, A. K. Coomaraswamy, W. B. Cranfield, Charles Daley, Rev. H. Purefoy Fitz-Gerald, Walter Garstang, James Hornell, F. H. B. Marsh, John Percival, G. H. Pethybridge, H. A. Potter, W. B. Scott, Herbert Stone, Iain N. C. Talman, Eleanor Vachell, L. Richmond Wheeler.

2 *Foreign Members by death.*—J. Hjort and A. Weberbauer.

3 *Associates* HONORIS CAUSA.—J. Ardagh, A. S. Kennard, V. V. Tchernavin.

7 *Fellows by Withdrawal.*—Rev. R. B. Abell, James Brady, G. Olds Cooper, D. I. Dawson, A. W. Exell, Norma M. Waterman, R. Whymper.

The number of Fellows on the List is 744 and 34 elected but not yet qualified. Since the last Anniversary Meeting, 61 Fellows, 2 Foreign Members, 2 Associates *honoris causa* and 3 ordinary Associates have been elected.

The Library.—Between the 1 May 1948 and 30 April 1949, 21 books have been purchased ; 24 books, 166 parts of periodical publications and 63 reprints have been presented. During the same period the number of volumes bound was 515, and 200 volumes have been repaired.

The number of volumes borrowed by Fellows and Associates was 1074 and by the National Central Library 424. 583 signatures were recorded in the Library Visitors' Book.

Linnaean and Smithian Collections.—During the past year the Linnaean Collections have been consulted frequently, the greatest number of consultations being those relating to the Herbarium. During the Summer of 1948, Dr. Arvid H. Uggla, R.N.O., R.V.O., A.L.S., of the Royal University Library, Uppsala, spent about three-and-a-half months here, working on his Catalogue of Linnaeus's Manuscripts.

Further progress has been made with the compilation of a Catalogue of the Smithian Herbarium.

THE PRESIDENT'S REVIEW.

It is a matter of great pride and satisfaction to me that during the period of my Presidentship, the number of candidates elected into the Fellowship has been 191, with the result that the number stands today at 779. This is very gratifying, but I hope that my successor will not consider that it is sufficient.

There are many reasons why I consider that the Fellowship of this Society should and can reach the number of 1000. It has always been the policy of the Council that the subscriptions should not be increased ; on the other hand, everything else, and particularly the cost of printing and publishing, has increased markedly. Every year, the Treasurer has to go, hat in hand, to the Parliamentary Grant-in-Aid, and ask for money to enable the Society to defray the cost of its normal publications. This would not be necessary if the Fellowship were just a little larger, and it is very desirable that it should not be necessary, and that the Society should be completely independent. One reason for this was apparent during the recent Conference on Scientific Information Services. At this Conference, some proposals were made that, in company with all similar societies, the publications should be taken out of the control of the Society and centralized and standardized in a national scientific publishing authority. These proposals were resisted and dropped, but it is evident that independence is the best guarantee of freedom.

There is another reason why it is of importance that the Society should be strong and capable of playing a leading part in the developing of biological thought, teaching and research in this country.

I may remind the Society that at the Anniversary Meeting held on 24 May 1945, my predecessor informed you that the then President of the Royal Society had invited the Presidents of those societies which had accommodation in Burlington House to meet him for the purpose of considering the problems raised by the shortage of space from which some of them were acutely suffering. At a meeting held on 26 May 1944 it was decided that a deputation should approach the Government, pointing out the need for additional accommodation and the importance of ensuring that scientific bodies were adequately housed in the capital.

In matters such as these it will readily be understood that discretion and patience are essential, and both were forthcoming. On 4 December 1947, the Royal Society convened another meeting to take stock of the situation. The representatives of the various societies present expressed views which indicated generally that those societies already housed in Burlington House would only be in favour of moving to other premises if all the principal scientific societies of the Kingdom could be housed in a group which would constitute a Science Centre. The various societies were invited to state what accommodation they would require if they moved to a new site, and to state the conditions under which they would be willing to support a move.

In reply to this questionnaire, which was, of course, still of a secret and confidential nature, the Council of the Linnean Society on 26 January 1948, gave the desired information as regards accommodation-space, and coupled it with a statement that the Society did not relish the prospect of vacating its present premises and sharing meeting rooms, council rooms, committee rooms, etc., with all the other Societies.

In November 1948, the London Press published some unofficial and ill-informed statements concerning the possibility of a move of the scientific societies to a site in Holland Park. I conceived it to be my duty to write to the President of the Royal Society and remind him that while I did not take these Press indiscretions very seriously, and without any prejudgment of the merits or demerits of this scheme or any other scheme, the necessity for discretion was responsible for the fact that the Linnean Society had never yet been invited to pronounce its opinion on the desirability or otherwise of its participation in any particular move. I took the opportunity of asking at the same time whether the position of those societies that might prefer to remain in Burlington House had been borne in mind and safeguarded.

The President of the Royal Society was good enough to answer and say that the position of the Linnean Society was well understood ; and I was interested to note that in his Anniversary Address delivered before the Royal Society on 30 November 1948, the President announced that the Fellows of that Society would be consulted on the major issue of policy as soon as it could be put to them in precise form. I have every confidence that at that time, which will I hope not be long delayed, the Fellows of this Society will likewise be provided with the opportunity of expressing their views on this most important matter.

The custody of the priceless collections around which we live makes us jealous of our independence and privacy, and, as in so many things, the price of freedom is eternal vigilance.

It only remains for me now to say how confident I am that in the wise choice which the Society has made of its new President, these difficulties will all be successfully surmounted and overcome. In relinquishing my office, I should like to say how grateful I have been to all members of the staff, to the Council, to the Library Committee, and to the Officers, for assisting me in accomplishing a task which has never failed to give me the greatest interest and pleasure.

The Financial Report was given by the Treasurer and the Accounts of the Society, duly audited, for the year 1948–49 were laid before the meeting.

TREASURER'S REPORT

Printed copies of the Treasurer's Accounts of the financial Year which ended on 30 April 1949 are before the Meeting. A Statement has been prepared by the Auditors who certify as to detail ; the Audit Committee has inspected the books, verified the investments and passed the accounts ; the action of the Committee has beeen confirmed by the Council.

Taking the payment side of the accounts first, there has been an increase of expenditure over last year of about £960. This sum is made up of the increased cost of heating, miscellaneous printing, and salaries, but mainly by the increased cost of publications which comes to £780 over last year. This was due to an increased cost of printing and more publications being issued than in the previous year.

On the income side the Admission Fees and Annual Contributions, owing to the increased number of Fellows, have increased by £397. Publications have again sold well. The sales amounted to £762, an increase of £69 over the previous year. The Society again received from the Royal Society as a grant in aid of Publications a sum of £750, and also a donation of £45 from Dr Jaramillo-Arango and a Legacy of £100 from the late Dr. Pethybridge. The Council have decided to place £900 to a Reserve for Publications for next year. This leaves a balance on the General Account of £558 to be carried forward to 1949-50.

The cost of publications in 1948-49 was £2126. The sum was made up by £360 from General Funds, £795 from the donations already mentioned, and the transfer of £1000 from the Publications Reserve. The Publications Reserve now stands at £1003, plus £900 put aside this year by the Council and totals £1903.

Turning to the Library Account it will be seen that the balance is £294, which includes £100 special donation for binding special books. On the same page is the account of the Library Restoration Fund. The receipts of this Fund have now reached £2993 and the money expended amounts to £1103. The two main expenses have been the steel shelving and the binding and repair of books. There is still much work to be done in the binding and repair of books and more money would have to be spent if it had not been for the scarcity of expert binders and repairers. A number of Societies and Fellows have subscribed to the Library Restoration Fund and I am sure all the Fellows will be duly grateful to them. There is still much to be done to bring the Library up to date and to a perfect state of repair for which money will be required for some years. I should like to appeal to all friends of the Linnean Library to help this Fund by donations and legacies in order that this historic Library can be maintained and conserved.

On the next page of the accounts are shown the special accounts. The Reserve Fund, money put aside during the war years to help with redecoration, etc. after the war, stood at the beginning of the year at £1286, it has now been spent or allocated to repairing and renewing the Central Heating, on redecorating and cleaning of the rooms and carpets. Our old heating apparatus was installed in 1873—so it had a long life.

On the last page of the accounts will be found the list of investments. There has been no change in these investments except the investment of the fees of those Fellows who have compounded their subscriptions. This amounts to £262 of which £258 has been invested in 2½% Consolidated Stock.

Finally, I should like to draw the attention of Fellows to the redecoration of the rooms, the cleaning of the Society's historic pictures, the provision of new shelving, renovation of the Library and the new up-to-date heating. This work has been carried out since the end of the war. Fellows can now work in the Library in comfort and many more Fellows have taken advantage of this. There is still much to be done in obtaining new carpets, etc. This will be completed as soon as our finances allow it and the prices of such necessities are not so expensive.

I should like to thank Mr. O'Grady our Clerk for the excellent manner in which the accounts have been kept. Mr. O'Grady carries out the detailed work in keeping the accounts and I am grateful to him for the conscientious way in which this work has been done.

If any Fellow wishes to ask any questions on these accounts, I will do my best to answer them.

On a motion by Lieut.-Col. W. P. C. TENISON, D.S.O., seconded by Dr. ERROL I. WHITE, the Report and Statement of Accounts were adopted.

TREASURER'S ACCOUNTS FOR THE

(Presented at the Anniversary

Receipts and Payments of the Linnean Society

General

RECEIPTS	£	s.	d.	£	s.	d.
To Balance at 1 May 1948 :—						
Current Account at Bank	117	18	3			
Deposit Account Post Office Savings Bank	456	8	0			
Cash in hand	7	5	1			
				581	11	4
,, Admission Fees				248	0	3
,, Arrears of Annual Contributions	88	0	0			
,, Annual Contributions for year	2465	15	8			
Do. in advance	59	2	4			
				2612	18	0
,, Do. of Associates				15	19	0
,, Composition Fees				262	0	0
,, Interest on Investments (including Income Tax recovered)				327	19	4
Do. Post Office Savings Bank Account				113	19	6
,, Sales of Publications :—						
Transactions	93	18	3			
Journals	491	5	1			
Proceedings &c.	177	0	9			
				762	4	1
,, Grant in aid of Publications				750	0	0
,, Miscellaneous Receipts				20	1	8
,, Transfer from Reserve for Publications Fund				1000	0	0
,, Donation.—Dr. Jaramillo-Arango				45	0	0
,, Bequest.—Dr. G. H. Pethybridge				100	0	0
				£6839	13	2

Library

	£	s.	d.
To Balance at 1 May 1948	126	10	9
,, Interest on Investments (including Income Tax recovered)	45	4	8
,, Donation	10	10	0
,, Transfer from General Account	300	0	0
,, Miscellaneous Receipts	2	7	0
	£484	12	5

Library

	£	s.	d.
To Balance at 1 May 1948	2615	0	0
,, Donations : Royal Horticultural Society	105	0	0
Imperial Chemical Industries	50	0	0
The Zoological Society	25	0	0
Fellows and Friends	198	6	0
	£2993	6	0

Fellows' Postal

	£	s.	d.
To Balance at 1 May 1948	50	6	5

Year ended 30 April 1949

Meeting, 24 May 1949)

from 1 *May* 1948 *to* 30 *April* 1949

Account

Payments	£	s.	d.	£	s.	d.
By Coal, Electric Current, and Gas				198	14	0
,, Repairs: Sundry				45	4	11
,, Taxes and Insurance				86	9	0
,, Miscellaneous Printing and Stationery				304	12	0
,, Petty Expenses and Postages				264	14	7
,, Publications :—						
Printing	2008	6	0			
Distribution	118	0	2			
				2126	6	2
,, Transfer to Reserve for Publications Fund				900	0	0
,, Salaries, Wages, etc. (including £66 10*s.* 0*d.* subsistance allowance to housekeeper during alterations)				1616	15	6
,, 'Zoological Record' (Vol. 84) Donation				15	0	0
,, The Biological Council—Donation				5	5	0
,, Staff Annuities (Annual Premiums)				100	0	0
,, Purchase of £326 8*s.* 7*d.* 2½ per cent. Consolidated Stock (Compounder's Fees)				258	17	3
,, Linnean Medal (1948)				4	10	5
,, Transfer to Library Account				300	0	0
,, Balance at 30 April 1949 :—						
Current Account at Bank	17	6	10			
Deposit Account Post Office Savings Bank	525	19	0			
Cash in hand	14	15	9			
Amount awaiting Investment	55	2	9			
				613	4	4
				£6839	13	2

Account

	£	s.	d.	£	s.	d.
By Periodicals				148	12	0
,, Binding				12	12	6
,, Books				28	14	6
,, Balance at 30 April 1949 :—						
Current Account	194	13	5			
Deposit Account Post Office Savings Bank	100	0	0			
				294	13	5
				£484	12	5

Restoration Fund

	£	s.	d.	£	s.	d.
Steel shelving				457	17	2
Glazing Bookshelves				90	0	0
Alterations (Library Annexe)				66	0	4
Purchase of Foreign Works				42	1	6
Binding and Repairs to Books				436	13	6
Miscellaneous				16	8	1
Balance at 30 April 1949 :—						
Current Account at Bank	262	15	5			
Deposit Account at Bank	621	10	0			
Deposit Account Post Office Savings Bank	1000	0	0			
				1884	5	5
				£2993	6	0

Account

	£	s.	d.
By Balance at 30 April 1949	50	6	5

Special Accounts
(Trust and Reserve Funds)

RECEIPTS

	£	s.	d.	£	s.	d.
To Balance at 1 May 1948 :—						
Westwood Fund	92	18	6			
Trail Award Fund	46	19	2			
Crisp Award Fund	83	5	2			
Hooker Lecture Fund	113	13	2			
Goodenough Fund	11	15	4			
Minchin Fellowship Fund	9	10	5			
Carnegie Corporation Grant	419	3	7			
Reserve Fund	1286	12	8			
Reserve for Publications Fund	2003	10	0			
Royal Society Grant (Dr. A. H. Uggla)	200	0	0			
				4267	8	0
,, Transfer from General Account :—						
Reserve for Publications Fund	....			900	0	0
,, Interest on Investments (including Income Tax recovered) :—						
Westwood Fund	10	17	4			
Trail Award Fund	3	10	0			
Crisp Award Fund	10	5	0			
Hooker Lecture Fund	21	18	0			
Goodenough Fund	8	12	8			
Minchin Fellowship Fund	3	0	0			
Staff Pension Fund	9	15	10			
				67	18	10
,, Deposit (Dr. A. H. Uggla)	....			15	0	0
				£5250	6	10

PAYMENTS

	£	s.	d.	£	s.	d.
By Reserve for Publications Fund :—						
Transfer to General Account	....			1000	0	0
,, Reserve Fund :—						
Central heating, repairs and cleaning	....			855	11	6
,, Staff Pension Fund :—						
,, Purchase of £9 9*s*. 4*d*. 3 per cent. Saving Bonds 1955/65	....			9	5	10
,, Dr. A. H. Uggla, Grant	....			200	0	0
,, Trail Award and Medals	....			35	2	6
,, Goodenough Fund to General Account	....			20	0	0
,, Minchin Fellowship	....			8	0	0
,, Balance at 30 April 1949 :—						
Westwood Fund	103	15	10			
Trail Award Fund	15	6	8			
Crisp Award Fund	93	10	2			
Hooker Lecture Fund	135	11	2			
Goodenough Fund		8	0			
Minchin Fellowship Fund	4	10	5			
Carnegie Corporation Grant	419	3	7			
Reserve Fund (for balance of cost of Central Heating)	431	1	2			
Reserve for Publications Fund	1903	10	0			
Dr. A. H. Uggla (Deposit)	15	0	0			
				*3121	17	0
				£5250	6	10

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* Including £3047 3*s*. 6*d*. in Post Office Savings Bank.

General Account

£	s.	d.			Market Value 30 April 1949. £	s.	d.
1000	0	0	3½ per cent. London County Consolidated Stock 1958–68	@107	1070	0	0
1548	8	9	British Transport 3 per cent. Guaranteed Stock 1978–88	@102½	1587	2	11
338	6	8	3½ per cent. War Stock	@103	348	9	8
1000	0	0	2½ per cent. Defence Bonds	@100	1000	0	0
2199	18	6	4 per cent. Australian Stock 1961–64	@112½	2474	18	4
200	0	0	3 per cent. War Stock 1955–59	@105½	211	0	0
1139	13	0	3 per cent. Savings Bonds 1955–65	@104	1185	4	9
2637	5	5	2½ per cent. Consolidated Stock	@ 81½	2149	6	5
176	19	3	3 per cent. Savings Bonds 1960–70	@103½	183	3	1
274	5	5	3 per cent. Treasury Stock	@100½	275	12	10
					£10484	18	0

Library Account

£	s.	d.			£	s.	d.
471	18	9	British Transport 3 per cent. Guaranteed Stock 1978/88 (Bentham Bequest)	@102½	483	14	8
103	12	5	Surrey County 3 per cent. Stock 1961–66 (Wakehurst Bequest)	@102	105	13	10
191	12	7	4 per cent. Australian Stock 1961–64 (Walker & Morey Bequests)	@112½	215	11	8
107	2	1	2½ per cent. Consolidated Stock (Stebbing Bequest)	@ 81½	87	5	9
530	0	0	3 per cent. Savings Bonds 1960–70 (Tagart Bequest)	@103½	548	11	0
					£1440	16	11

Special Accounts

	£	s.	d.			£	s.	d.
£1063 10 7	232	5	0	Metropolitan Water Board 3 per cent. " B " Stock (Westwood Bequest)	@100	232	5	0
	667	14	2	Ditto ditto (Hooker Lecture Fund)	@100	667	14	3
	163	11	5	Ditto ditto (Goodenough Fund)	@100	163	11	5
	100	0	0	New South Wales 3½ per cent. Stock 1930–50 (Trail Award Fund)	@102½	102	10	0
	409	11	1	2½ per cent. Consolidated Stock (Crisp Award Fund)	@ 81½	333	15	9
£380 10 6	156	7	2	,, ,, ,, (Westwood Fund)	@ 81½	127	8	8
	74	14	6	,, ,, ,, (Hooker Lecture Fund)	@ 81½	60	18	0
	149	8	10	,, ,, ,, (Goodenough Fund)	@ 81½	121	15	11
	277	9	6	3 per cent. Savings Bonds 1955–65 (Staff Pension Fund)	@104	288	11	6
	100	0	0	,, ,, ,, 1960–70 (Minchin Fund)	@103½	103	10	0
						£2202	0	6

F. C. STERN, *Treasurer.*

We have (in conjunction with the Professional Auditors, who certify as to all details) audited the Accounts of the Society for the year ended 30 April 1949 and found them correct. We have verified the Investments and Bank Balances.

19th May 1949.
W. B. KEEN & Co., *Chartered Accountants*,
Finsbury Circus House,
Blomfield Street, London, E.C.2.

G. R. DE BEER,
A. H. G. ALSTON,
B. BARNES,
I. HENRY BURKILL,
A. TINDELL HOPWOOD,
H. W. PARKER,
ELSIE M. WAKEFIELD,
Audit Committee.

The PRESIDENT then delivered his Address on 'Caruncles and Egg-teeth: some aspects of the concept of Homology'.

On its conclusion, Lieut.-Col. R. B. SEYMOUR SEWELL, C.I.E., F.R.S., moved 'That the President be thanked for his excellent Address, and that he be requested to allow it to be printed and circulated amongst the Fellows'. The motion was seconded by Dr. A. d'A. BELLAIRS, and being put to the meeting was carried with acclamation.

The PRESIDENT then declared the Session of 1948–49 ended.

PRESIDENTIAL ADDRESS

By Professor G. R. DE BEER, F.R.S., P.L.S.

CARUNCLES AND EGG-TEETH: SOME ASPECTS OF THE CONCEPT OF HOMOLOGY.

(Plates **13–15**, and 1 text-figure.)

The mark of a good poet, according to Aristotle, was the skill with which he used metaphor. Metaphor is a descriptive device designed to give a vivid picture of the object or event in question by resorting to analogy; and analogy is based on the discernment of a similarity between the object or event in question and those are used as the metaphor. I consider that it is no accident that the first person in modern times to have raised the similarities that may be discerned in different living organisms to the level of a subject that may be studied for its own sake, was a poet: Johann Wolfgang Goethe, the bicentenary of whose birth is being celebrated in this year; and the subject is that to which he gave the name of *morphology*.

Morphology is the study of the structure of an organism in terms of the unity of plan of the group to which it belongs; it is the reward of comparative anatomy, and provides for a certain amount of intellectual comfort in the face of the bewildering number of organic forms by permitting a reduction in the vastness of their multitude to a relatively small number of so-called types. And while organisms of a group may show a unity of type, their parts may show a similarity which morphologists recognize as *homology*.

Goethe's presentation of the concept of homology has a remarkable dynamic character which has been lost from the lucubrations of most of his successors. It is found in his work on *The Metamorphosis of Plants*, published in 1790, of which an admirable translation and analysis has recently been given by Dr. Agnes Arber, F.R.S., to whom this Society was proud to award the Linnean Medal in 1948. As she has shown, Goethe attempted to explain the manifold structures presented by a living plant on the supposition that an appendage like a foliage leaf has undergone metamorphosis or, in simpler language, been changed in the production of other appendages such as the bracts and the parts of the flower.

It has been pointed out that such a use of the term metamorphosis is figurative, since no actual change of an appendage of one type into another is witnessed; it is inferred that if, as appears to be the case, there is an underlying similarity between the various different types of appendage, then the change from the production of one to the production of another type reflects a corresponding change in the formative processes that are at work. It is of some interest to note this dynamic quality of Goethe's concept, for in the hands of his successors the idea of homology was frequently to connect the final results of morphogenesis rather than processes of morphogenesis themselves.

Even were I competent to do so, it is not my purpose here to inquire how far Goethe's leaf-theory is regarded today as an adequate formulation of the problems of plant morphology. On one point, however, there will be general agreement, that it has served a useful purpose in stimulating research.

If now we turn to the animal kingdom, we shall find that Goethe's application of his principles led him to two sets of results; the one most acceptable, as when, starting off from the observation that mammals have a premaxilla, deducing that since man is a mammal he ought to possess a premaxilla, and then verifying this proposition by actual observation in early stages of development: the other unacceptable, as when, starting off from the superficial resemblance that a broken rabbit's skull bears to a number of vertebrae, he supposed that the skull in vertebrates was a modified set of vertebrae. This supposition was not in accordance with the facts and fell shattered for ever by Huxley's devastating criticism.

FIG. 1.

FIG. 1.—Johann Wolfgang Goethe, in front of his house on the Frauenplan at Weimar. (*Goethe Nationalmuseum, Weimar.*)

The different fates of these two excursions by Goethe into animal morphology illustrates one of the most important principles which should be followed when considering problems of this kind. It is that the value of an hypothesis regarding the possible homology between the parts of organisms stands or falls by an appeal to the facts of the detailed structure of the parts in question.

If it can be shown that two parts or structures in different organisms despite differences of a trivial or superficial nature involving detailed shape, size, or position, nevertheless show a similarity in the three dimensional geometry of their relations to the neighbouring structures, i.e. a similarity of morphological relations, it is usual to accord to such parts the status of homologous parts. This is, in essentials, the criterion which was recognized by E. Geoffroy St. Hilaire and by Richard Owen.

As my friend Professor J. H. Woodger has aptly observed, the performance of a comparison between the anatomies of two organisms involves a number of operations which are only too often taken for granted. For one thing, the two animals, if such they be, must be placed in correspondence, head to head, and dorsal surface to dorsal surface. Unless this is done, no great benefit is likely to result from any comparison, and it is interesting to consider for a moment why it is that comparative anatomy should be dependent on a show of ' goodwill ' in presenting the terms of the comparison under conditions that are as favourable as possible. There is a good precedent for mistaking the two ends of an animal ; I refer not only to the elephant that does not accept the proffered bun, but to the tape-worm.

What are the principles by which the morphologist should be guided in laying out his material so as to reveal the most profitable correspondences ? It cannot be left to pure hazard or there might result countless absurdities, as if one tried to compare the tail of a cat with the foreleg of a dog. The fact that in this particular case any other procedure would be absurd, is no justification for refraining from inquiring into the general principle underlying the action to be taken in all cases. Nor is it legitimate to adopt as a principle the placing of the two animals in such a position as to produce the maximum number of correspondences. For while there might be little room for manoeuvre in such a procedure if the two animals were as similar as cat and dog, it would involve empirical considerations and subjective decisions if the animals were markedly different, as, say, a rabbit and a tape-worm. Most important of all, such a procedure would take for granted one of the most important questions to be solved.

I suggest that in this field we have another instance of the debt in which biologists stand to Charles Manning Child, For.Mem.L.S. He showed that the practice of putting first things first had an objective meaning in embryology, in that the prime determination in time and in importance which is effected in an organism is that of the axis of polarity, the determination of which is the future anterior end. Once this determination has been made, two organisms can be placed in correspondence, even if one be only a sea-anemone and the other a mammal. But all organisms above the sea-anemones undergo a second major determination, which is that of the plane of bilateral symmetry, the determination of which is to be the future dorsal surface, by which of course all the other sides are likewise determined. Once this determination has been effected, the animal is ' set ' as regards the three axes of space, and can be placed in correspondence with any other animal.

This may appear such a truism as to seem almost tautological. On consideration, however, it will, I think, be apparent that this view does, in however simple a form, attempt to provide an independent criterion of the principles on which comparisons can be made. For comparisons of greater refinement relating not to entire animals but to parts of animals, other independent criteria of reference must clearly be called into play. These remain to be determined.

It will have been noticed that I have, so far, said nothing about the bearing on the problem of homology of the historic fact of evolution. There is, of course, a body of opinion that considers that the perfect definition of homology should rest on community of descent from a common ancestor. Such a view, while perhaps ideally desirable, suffers from three difficulties. The first is that in most cases the common ancestor of two different forms is unknown, and an appeal to it as a basis for the decision as to the homology or non-homology of two sets of parts is speculative, and not to be preferred to the objective resort to detailed comparative anatomy.

The second difficulty is the situation brought about by the possibility that two sets of parts or structures in two different though related organisms, may show all the criteria required for homology on grounds of comparative anatomy, but the parts or structures may be demonstrably lacking from the common ancestor. This curious state of affairs applies to the horns on the heads of Titanotheres. The ancestral forms were small and hornless. In a number of separate lines of descent the size of the body became larger and horns appeared, independently. Huxley has shown that this result is explicable in terms of allometric growth-control; its importance from the present point of view is the fact that to deny historic affinity between these structures on the sole ground that they were not visibly manifest in the common ancestor, would be to deny genetic affinity and a common predisposition to form the structures in question, in cases where it is reasonable to suppose that community of descent is marked.

The other difficulty is of a logical nature, though it should not be over emphasized. Since homologous parts are used to determine the identity of the common ancestor, that common ancestor should not be appealed to for the purpose of deciding whether two sets of parts are homologous. If the problem were as simple as this, there would be no need for argument. But homologous parts can often be numbered not in ones and twos, but in dozens or in hundreds, between two organisms. Indeed, the more homologous parts there are in two organisms, the more closely they are held to be related. By means of the morphological determination of a large number of homologous parts, say 99, a good approximation can be obtained to the probable appearance of a common ancestor. And if now a 100th pair of parts be considered, it is surely permissible to consider it in terms of descent from the common ancestor as conjured up by means of the other 99. If, then, there is in two animals a sufficiency of parts whose homology has been determined by means of the criterion of comparative anatomy, it is not illegitimate to consider the possible homology between other parts in the light of presumed descent from a common ancestor. As will shortly appear, such a process of reasoning will also have to take into consideration the probability or otherwise that structures can have had independent origins, have been lost, or re-developed.

Meanwhile, attention may be turned to a few features presented by the problem of homology which it is useful to bear in mind. First, the impossibility of taking as a criterion of homology any identity of position in the egg of the presumptive region from which homologous structures may be developed. The annals of embryology are replete with examples of differences in the way in which the same result is achieved during development. Similarly, to attempt to attribute the formation of homologous structures to similar morphogenetic processes likewise breaks down. The lens of the eye in one species of frog may be dependent for its formation on the presence of the eye-cup; in another species of frog it may be independent; but no one would for that reason dream of denying the homology between the lenses. Lastly, in spite of the fact that homologous structures and parts must be conceived as having a community of descent from a common ancestor, it is not possible to ascribe the cause of their similarity to an identity of the genes which control their appearance, for there are many examples of homologous structures which can be shown to be under the control of different genes, while identical genes are known to be capable of controlling structures which are not homologous. I have dealt with these and kindred problems at sufficient length elsewhere to allow me to dispense with the necessity of repeating myself.

I turn therefore to some aspects of the problem of determination of homology by means of comparative anatomy, as illustrated by the egg-tooth and the caruncle, structures which play an important part in the life-history of many vertebrates in which they enable the embryo to pierce the embryonic membranes, break the shell and emerge as free-living animals.

The adaptations to enable embryos to hatch have been numerous and various in the vertebrates. In some cases, as in those of certain teleost fish and anuran amphibia, specialization of the epidermis in the region of the snout to form a gland secreting proteolytic enzymes results in the chemical digestion of the egg-membrane and its easy rupture. In *Leiopelma*, as Mr. N. G. Stephenson has recently shown before this Society, the muscular tail serves to rupture the egg-membrane. Here, however, I propose to confine myself to a consideration of mechanical means of membrane- and shell-rupture involving the presence of horny epidermal caruncles and/or dentinal egg-teeth.

That adaptations of this kind have arisen repeatedly and independently can be shown by reference to the Amphibia. In *Eleutherodactylus abbotti* Noble has shown that on the under surface of the snout there is a little anvil-shaped epidermal structure, the sharp points of which serve to pierce the egg-membrane. An arrangement similar in principle but very different in detail, is found in *Rana opisthodon* (Plate **13**, fig. 1; Plate **15**, fig. 1). In this form, as I have been able to satisfy myself, through the kindness of Mr. H. W. Parker, who has made a specimen available to me, there is an epidermal spike at the very tip of the snout, and it is supported by a massive median cartilaginous rostrum extending forwards from the skull in a manner which so far as I know is unique in the Anura. On grounds of comparative anatomy therefore, I feel that the horny caruncles of *Eleutherodactylus abbotti* and *Rana opisthodon* do not qualify as homologous.

Coming now to the reptiles we find that (Plate **14**, figs. 1–5) in *Sphenodon*, the Chelonia and Crocodilia, as well as in the birds, there is on the upper surface of the snout, near its tip, a conical projection formed by a great development of the epitrichial layer of the epidermis. This is the well-known caruncle, to which it is important to refrain from giving the name ‘ egg-tooth ’. The similarity of its position and of its structure in the types mentioned combine to justify the view that the caruncle is homologous in all these four groups.

Very different is the situation in the remaining groups of reptiles, namely the Lacertilia and the Ophidia (Plate **15**, figs. 2–7; Plate **13**, fig. 2). In these, there there is no caruncle, but the foremost teeth or tooth of the upper jaw are or is modified, directed forward, formed precociously and enlarged, with the result that by projecting forwards beyond the tip of the snout, a razor-sharp structure is available which can serve to pierce or slash not only the egg-membrane, but also the leathery shell.

It is perfectly clear that there is no homology whatever between the caruncle and the egg-tooth, but even among the animals which show typical egg-teeth there is remarkable variation. For instance, in *Hemidactylus*, there are paired symmetrical egg-teeth, of equal size, both projecting forwards. But in *Lacerta vivipara*, only the right hand member of the foremost pair of teeth is enlarged and projects: the left hand member remains of the ordinary size of the normal teeth. In another form again, *Lygosoma*, instead of showing a paired structure, the egg-tooth is median and single. The same is true in the Ophidia.

There can be no doubt that the egg-teeth of all these forms are homologous, and yet we find that they may be paired in some forms and median and unpaired in others. Sufficient is known of the possibilities (well shown by the work of P. M. Butler) of variation in time and space during development of teeth for this conclusion to be readily accepted by embryologists and morphologists today, although it might have shocked our predecessors.

At the same time, there is, in the material so far presented, evidence that the variations must also be regarded as having taken place independently in different groups. The egg-tooth is median and unpaired in such lizards as *Lygosoma* and also in the snakes; but it is impossible to conclude that the snakes are more closely related to *Lygosoma* than they are to the other Lacertilia. Indeed, it would appear most probable that the paired condition of the egg-tooth as shown in *Hemidactylus* may be the original condition. I know that this is not the opinion of my distinguished colleague, Professor Martin Woerdeman, because he considers that the paired egg-teeth of *Hemidactylus* belong to a different generation of teeth than the asymmetrical or median egg-tooth of other lizards, and because he believes that he has found the vestige of a median egg-tooth between the paired egg-teeth in the geckos. In view of the fact that homologous structures such as arms and legs can undoubtedly arise at different levels along the length of animals, and teeth of a particular type of differentiation such as incisor or molar may be formed at varying levels in the mouth, it follows that the pattern of a differentiated structure is of more fundamental importance than its precise position. And for this reason I should not like to deny the homology between the egg-teeth of different lizards because they belonged to different tooth generations.

Be that as it may, and whether the paired condition of the egg-teeth in *Hemidactylus* is primitive or secondary, there can be little doubt that the median nature of the egg-tooth in *Lygosoma* and in the snakes must be secondary and that it must have arisen independently in each case from a condition in which the egg-teeth were paired.

I now come to a condition that presents considerable interest, namely, that of the monotreme. As Professor J. P. Hill has been able to show in the course of a research in which I have been privileged to collaborate with him, the monotremes are unique in possessing not only an egg-tooth (which is median and unpaired), but also a caruncle. However, this caruncle differs from that of the reptiles in its structure. For whereas the caruncle of reptiles is formed entirely by a thickening of the epidermis, in the monotremes the epidermis is only slightly thickened and the major part of the structure is composed of a massive dermal core containing a nodule of bone, the os carunculae.

The question immediately arises whether this monotreme caruncle can be regarded as homologous with that of the reptiles. If the canons of comparative anatomy are applied rigorously, then it would have to be concluded that they are not. On the other hand, it is not very difficult to imagine that a process of substitution may have occurred during evolution, and that there has been a progressive replacement of the epidermal constituent of the caruncle by dermal components. I believe that there are comparable cases to be found in the scales of lizards where a bony knob may be formed beneath the scale and may overtake it in size.

In any case, this is the moment to draw attention to the warning which I have already sounded earlier in this study. It is that the concept of homology will cease to have any value, and indeed will defeat its own ends, if it leads to the acceptance of conclusions in advance of adequate objective information. The real function of the concept of homology in this case is to appeal to observers to provide this information. Slender as the chance may be, it might be possible for some facts relating to the caruncle to be obtained from the study of the eggs such as those of the dinosaurs which have been discovered in comparatively recent times. And even if the concept of homology does nothing more than to awaken interest in the structures the homology of which is in question, science will benefit from it.

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EXPLANATION OF LETTERING.

ap, ascending process of premaxilla; *be*, buccal epithelium; *ble*, basal layer of epidermis; *c*, caruncle; *dl*, dental lamina; *et*, egg-tooth; *lj*, lower jaw; *lp*, left premaxilla; *mce*, modified cells of epidermis; *nb*, nasal bone; *ns*, nasal septum; *ol*, olfactory lobes; *p*, pulp of egg-tooth; *pm*, premaxilla; *rp*, right premaxilla; *rt*, rudiment of normal tooth; *sc*, stratified cells of epidermis; *sp*, suture between premaxillae; *uj*, upper jaw.

EXPLANATION OF PLATES.

PLATE 13.

FIG. 1.—*Rana opisthodon.* Dorsal view of head of embryo at time of hatching, showing the tip of the snout, supported by an extension of the cartilaginous nasal septum forming a rostrum. In this photograph the epidermis has been ruptured and the rostrum is projecting. [Through the kindness of Mr. H. W. Parker, F.L.S., Keeper of Zoology, British Museum (Natural History).]

FIG. 2.—*Python molurus*, 5 days after hatching, showing the egg-tooth.

PLATE 14.

FIG. 1.—*Sphenodon punctatum.* Median longitudinal section through the anterior end of the head of an embryo showing the caruncle. [Dendy collection, King's College, London, by the kindness of Professor Doris Mackinnon.]

FIG. 2.—*Chrysemys marginata.* Horizontal section through the head of an embryo showing the caruncle.

FIG. 3.—*Alligator*, sp. Median longitudinal section through the head of an embryo showing the caruncle.

FIG. 4.—*Gallus bankiva.* Median longitudinal section through the tip of the beak of a chick embryo of 20 days' incubation showing the caruncle.

FIG. 5.—The caruncle of Fig. 4 under higher magnification.

PLATE 15.

FIG. 1.—*Rana opisthodon.* Paramedian longitudinal section through the head of an embryo at time of hatching, showing the massive cartilaginous projection of the nasal septum to form a rostrum supporting the caruncle. [Through the kindness of Mr. H. W. Parker, F.L.S., Keeper of Zoology, British Museum (Natural History).]

FIG. 2.—*Hemidactylus fasciatus.* Transverse section through the anterior region of the upper jaw of an embryo, showing the paired egg-teeth of equal size.

FIG. 3.—*Hemidactylus fasciatus.* Transverse section posterior to that shown in Fig. 2, to show the origin of paired egg-teeth from the dental lamina. [2 and 3 are from the collection of Dr. Angus Bellairs, F.L.S., by his kind permission.]

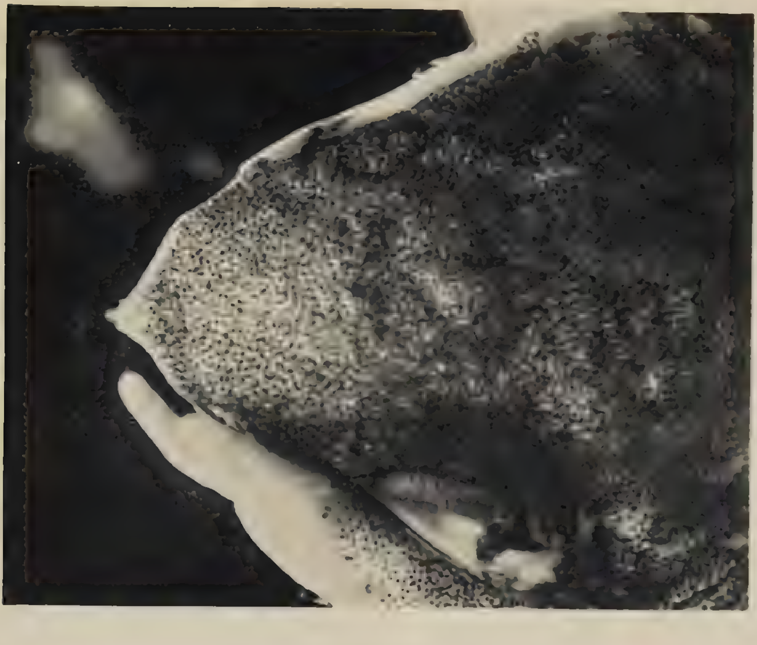
FIG. 4.—*Lacerta vivipara.* Transverse section through anterior region of the upper jaw of an embryo, showing the single asymmetrical egg-tooth on the right-hand side.

FIG. 5.—*Lacerta vivipara.* Transverse section posterior to that shown in Fig. 4 to show the paired nature of the tooth rudiments of which the right-hand member is enlarged to form the egg-tooth. [4 and 5 are from the collection of Dr. Angus Bellairs, F.L.S., by his kind permission.]

FIG. 6.—*Lygosoma guichenoti.* Transverse section through the anterior region of the upper jaw of an embryo to show the single median egg-tooth.

FIG. 7.—*Tropidonotus natrix.* Transverse section through the anterior region of the head of an embryo to show the median unpaired egg-tooth.

I should like to ackowledge the assistance which I have constantly received in the preparation of this work from Mr. F. J. Pittock, F.R.P.S., A.L.S., who has taken the photographs, and Mr. H. Barker, who has cut many of the sections. For material I am likewise indebted to the kindness of Professor Doris Mackinnon, Mr. H. W. Parker and Dr. Angus Bellairs.



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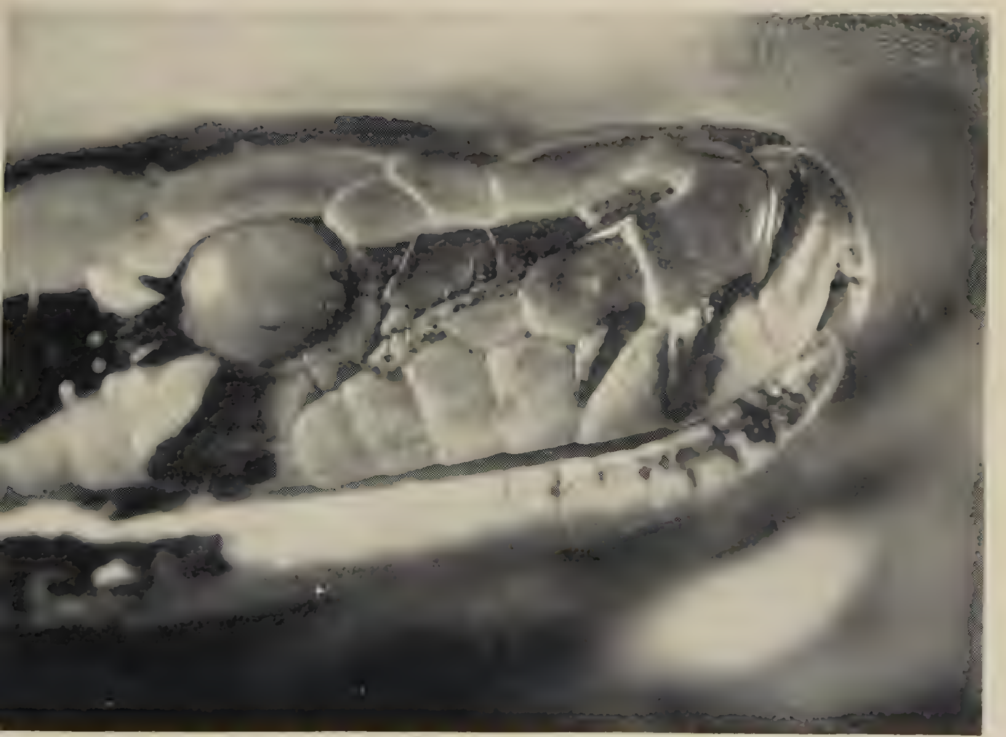

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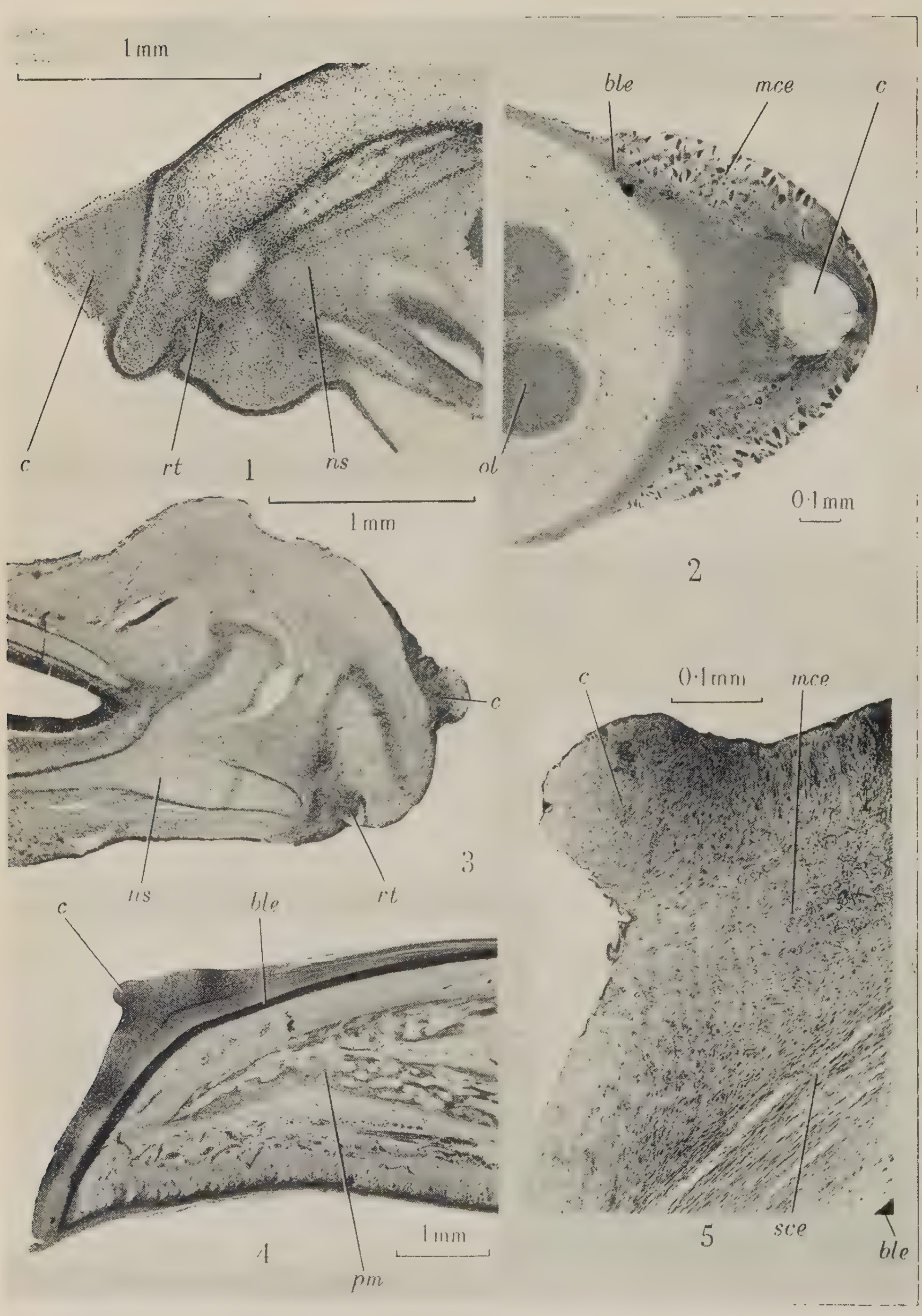
CARUNCLES AND EGG-TEETH



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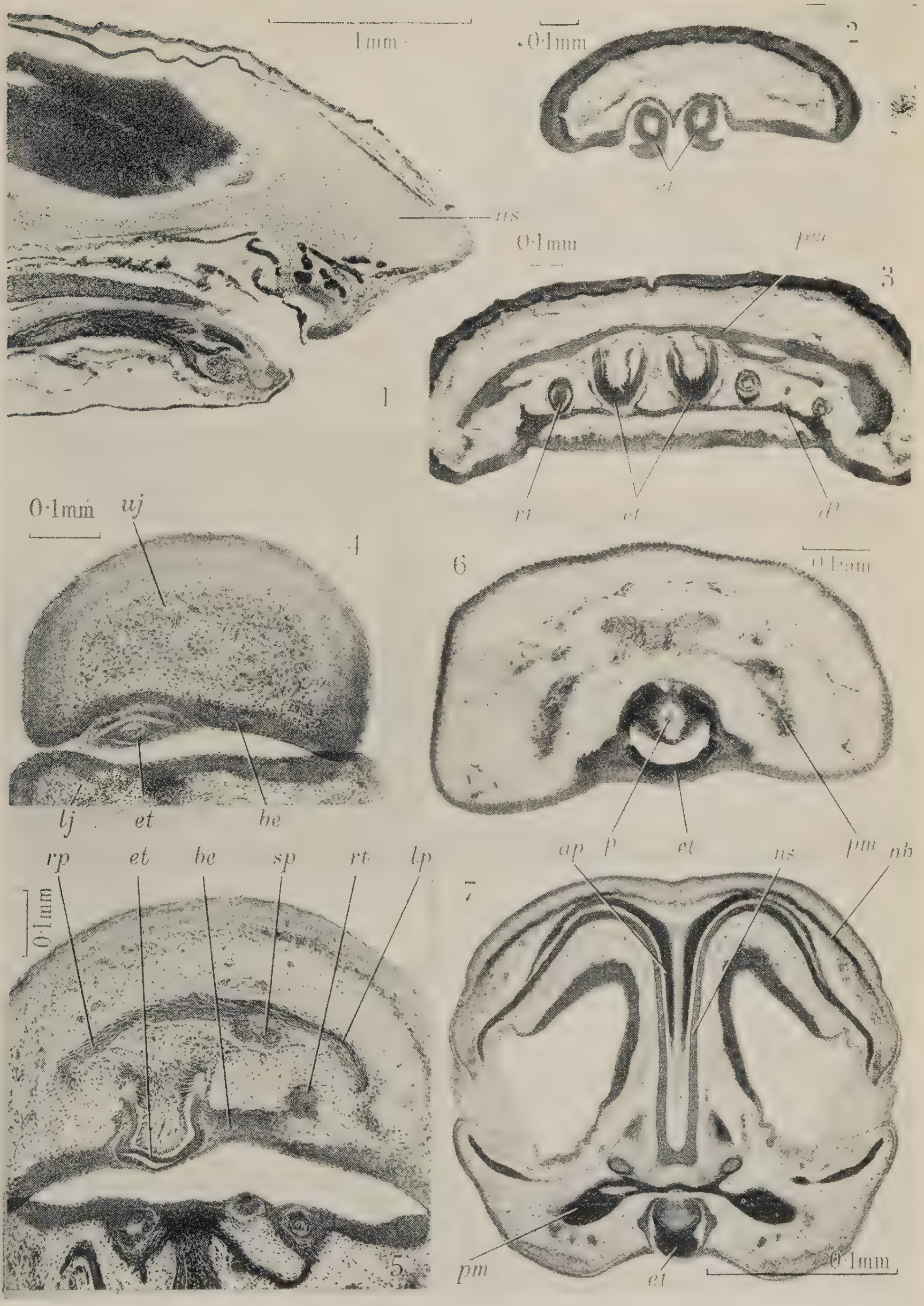

CARUNCLES AND EGG-TEETH

THE CORRESPONDENCE BETWEEN LINNAEUS AND JOHANN GESNER

By G. R. DE BEER, F.R.S., P.L.S., F.Z.S.

(Plate **16**)

[Read 10 March 1949]

The brilliance with which the star of Albrecht von Haller blazed over the whole of Europe inevitably resulted in the partial eclipse of others, both in his time and since. This was the case with his countryman Johann Gesner (1709–1790) of Zurich, a descendant of a relative of the great Conrad Gesner. I am absolved from the duty of describing Johann Gesner's life and career, for he has done it himself in the letters which follow. Linnaeus has done the same in his letters to Gesner, and the value, importance and charm of this correspondence lies in the simple manner in which these two great men introduce themselves to each other, describe their methods of work, their progress and difficulties, and give an account of the state of biological sciences in their respective countries. Gesner's portrait is shown in Pl. **16**.

The letters from Gesner to Linnaeus (which reached their destination) are in the Linnaean Correspondence in the Society's possession. Those from Linnaeus to Gesner have had a more chequered history. Dr. Rudolf Steiger, Librarian of the Zentralbibliothek in Zurich, has very kindly drawn my attention to a passage in the work of Rudolf Wolf * which runs as follows:—

'It is unfortunate that Paul Usteri did not carry out his intention of publishing Gesner's correspondence, and it has since been dispersed. Nevertheless, a considerable portion is to be found in the rich collection of autographs belonging to Herr Ott-Usteri in Zurich, and the collection of letters which I made for the Swiss Natural History Society also contains some.'

Herr Steiger has further informed me that the catalogue of the Ott-Usteri collection contains an entry for one (unspecified) letter from Linnaeus to Gesner, but it was already missing when the collection was acquired by the Zentralbibliothek. Similarly, Wolf's collection of letters, as also many of Gesner's manuscripts and papers, have disappeared.

The situation has been partially saved through the purchase in Berlin by the Royal Library of Upsala of two of the Letters from Linnaeus to Gesner. Through the kindness of Dr. Arvid Hjalmar Uggla, A.L.S., lately librarian of the Royal Library, they are reproduced here. Dr. Uggla has also very kindly given the reference to the third and last letter of which only a fragment is known, which is here transcribed from the 'Catalogue of the Collection of Autographed Letters and Historical Documents formed between 1865 and 1882 by Alfred Morrison compiled and annotated under the direction of A. W. Thibaudeau, vol. III, K–L, Printed for Private Circulation, 1888'. Messrs. Quaritch have kindly informed the Librarian that this letter was not included in the sale of the Morrison MSS., and its whereabouts are unknown. I wish to express my gratitude to Mr. Savage for his constant and invaluable help.

It will be noticed that several letters (including that of 4 November 1748 from Linnaeus) are still missing, and it is to be hoped that they may one day be found. But enough have been preserved to tell a complete, consistent and fascinating story.

I am indebted to Dr. R. D. McLellan and Mr. J. A. Willis for assistance in translating the (often obscure) Latin of these letters into English. I am also conscious of the decadence involved in substituting English for the then-universal language in which they were written. I can only plead that since latin is greek to so many today, more are likely to enjoy the interest of these letters in English than if I had published them in their original form, or than if they had been translated into Swedish or German.

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* *Biographien zur Kulturgeschichte der Schweiz,* Zürich, 1858, vol. 1, p. 319.

I. *Linnaeus to Gesner*, 8 *Aug.* 1742. [Uppsala Univ. Libr. MS. G.152*a*.]

To the most celebrated gentleman,
Mr. Johann Gesner, Professor at Basle,
from Carl Linnaeus.

Not one but several letters from the learned Dr. Gronovius[1] have informed me of your particular benevolence towards me, most illustrious Sir. I have long wished to correspond with you, not only because you are my real patron and a genuine student of Flora, but also because you live in the most prolific of all the regions of Europe.

Since the death of Johann Scheuchzer[2] of blessed memory, I have had no communication with any of your countrymen ; do not therefore take amiss what I shall ask of you.

After leaving the Low Countries and travelling through part of France, I returned home and was presently appointed Medical Officer in the Navy, where I was each day overwhelmed in treating an immense crowd of sick.

At length I obtained the blessing of leisure after I was promoted to the professorship of medicine and botany at Upsala. During this summer I have been fully occupied in restoring the ruined garden of the academy ; the hot-houses (or orangeries) and the professor's house have this year been splendidly rebuilt, where with God's grace I shall spend the rest of my life.

I have just introduced into the garden all the Swedish woodland and indigenous plants ; I have acquired all the exotic plants, however few, that I have been able to find in the gardens of the nobility of Sweden ; and I have been enriched by the generous hands of de Jussieu[3], Gronovius[1], Royen[4], Barrère[5], Sauvages[6], and Amann[7], each of whom sent me many seeds.

Oh how I wish that I were able to visit your treasures, your most blessed Alps ! In the whole garden I have succeeded in obtaining not a single alpine plant save only Betula foliis orbiculatis. I wish that I might be able to buy seeds of alpine plants from you, at whatever price you choose. If you should ask which, I answer that you can send me some from every plant of the Alps. If you agree, I beseech you thrice to send the seeds included in a letter under cover addressed to the Royal Society of Letters and Sciences of Upsala. Each one of them when they germinate will remind me of you whenever I look at them.

Pray tell me the dates of the birth and death of Johann Scheuchzer[2] and of Johann Amann[7], and also what researches in botany by you will be published, and what new botanical works.

I am wholly occupied in describing the *Species of Plants*, where I refer all the species that I know to their genera with the specific differences, varieties, and localities.

---

[1] Johan Frederick Gronovius, 1690–1760.

[2] Johann Scheuchzer, 1684–1738.
The Zentralbibliothek Zurich possesses two autograph Latin letters from Linnaeus to Johann Scheuchzer, one dated 8 March 1737, the other undated but probably of the same year

[3] Bernard de Jussieu, 1699–1776.

[4] Adriaan von Roÿen, 1705–1779.

[5] Pierre Barrère, 1690–1755.

[6] François Boissier de la Croix de Sauvages, 1706–1767.

[7] Johann Ammann, 1707–1741.

JOHANN GESNER (1709–1790)

I am about half-way through with the catalogue of all the animals, quadrupeds, birds, fishes, insects and worms of the Kingdom of Sweden that I know, with their synonyms.

Fare you thrice well and love me.

Given at Upsala, 1742,
8th day of August.

(Address :)
To the most celebrated gentleman,
Dr. Johann Gesner,
Professor at Basle,
by Hamburg,
to Basle.

II. *Gesner to Linnaeus*, 30 *Oct.* 1748. [Linnaean Corr., Linn. Soc. Lond.]

To the Prince of Botanists, the most Illustrious and Excellent Carl Linnaeus, Professor of Medicine and Botany at Upsala—Greetings from Johann Gesner.

The several assurances of your kindness which I have received, Honoured Sir, have encouraged me to write to you with the greater confidence. I first became acquainted with your benevolent attitude towards myself and my writings through a letter from our common friend the celebrated Gronovius[1], secondly through your own most courteous letter dated the eighth of August 1742, and finally from the letters and conversation of Gmelin[2], whose services to botany are so great. There is nothing which I esteem more highly than your favour: but I shall seem to have made a poor reply to your kindness to me, since hitherto you have received from me no token of my gratitude, not even a letter. I trust you will allow yourself to be persuaded that in this matter the blame is not mine, since there can be no doubt that the letters perished in transit. Yours also must have suffered a like fate, which you addressed to me at Basle, when I was residing at Zurich. Now however I am taking advantage of the opportunity kindly afforded me by the learned Gmelin, to send a letter from which you may learn how highly I value your favour, and what respect I feel for your contributions to medicine and natural history, and so that you may become acquainted with our efforts and exertions, which I earnestly beseech you to take under your guidance.

From my youth upwards I burned with an incredible zeal for botanical studies, which my parents observed, and concluding it to be inborn in me, entrusted my training to the illustrious Jacob Scheuchzer[3], on whose words and instructions I hung for several years, and from whom I gained some knowledge of plants, albeit of an empirical nature. Before I was seventeen years old I had climbed the most remote of the Swiss Alps in search of specimens: and in 1726, going to Basle and to Leyden, I made the acquaintance of the immortal Boerhaave[4], whose paternal affection towards me I shall not cease to remember with gratitude as long as I live. At the same time, as a result of his great kindness, I had continuous access to the most magnificently laid out gardens of the University, while I enjoyed at once the benefits of his tuition and of his advice. Greatly did I profit also by the outstanding kindness and friendship of the celebrated Gronovius, through whose liberality I gained an acquaintance with many of the rarest plants which he sent to me out of his garden and his collections.

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[1] Johan Friedrik Gronovius, 1690–1760.

[2] Johann Georg Gmelin, 1709–1755.

[3] Johann Jacob Scheuchzer, F.R.S., 1672–1733.

[4] Herman Boerhaave, 1668–1738.

At Paris I received much assistance from the brothers de Jussieu[5] and from Isnard[6], but after a winter devoted to anatomy and surgery, I lay ill for four months with a fever, and having with difficulty recovered my health, was drawn back by paternal affection to Switzerland. At Basle once again I studied mathematics for two years under the well-known mathematician, J. Bernouilli[7], having as a fellow-student in the first year the celebrated Haller[8], whose close friendship I had enjoyed at Paris and Leyden. This famous man then began to take the greatest interest in plants, and in 1728 asked me to accompany him on a journey through the district of Basle, part of the Jura mountains, Geneva, Mt. Salève and the Valais[9]. On my return in the same year I practised medicine in Zurich, and gave instruction in mathematics, physics, medicine, anatomy and botany; always devoting such spare time as I had to my beloved flowers.

At this time I began to collect material for a methodical Synopsis of Swiss Plants, a work in which I enjoyed the encouragement and assistance of my dear friend Haller, with whom I exchanged specimens of rarer plants and observations, he taking for his province Savoy, the Valais, and Berne, while I took Schwyz, Uri, the Rhaetian Alps, Appenzell, and the mountains of the Toggenburg. In the years 1733 and 1734 I spent the summers in the Alps. In 1734 I succeeded Jakob Scheuchzer[3] as teacher of mathematics, and his brother Johann[10], the celebrated authority on grasses succeeded him in the profession of physic and in the dignity of Canon, a distinction which even the great Jakob Scheuchzer was not able to enjoy for more than four months. While Johann was absent and engaged in political affairs I acted as his deputy in giving instruction in physic. In 1735, after suffering from an obstruction of the liver, I sought and by God's kindness found relief in the distant Baths of Leuk, where I gathered plants from the surrounding mountains, and on my return began to lay more detailed plans together with my dear Haller for our synopsis of plants, which, in a shortened form, was even then in the hands of my students. But since I was still feeling the effects of my old malady, and had greatly suffered from the change of climate, my parents and friends persuaded me to say farewell to Alpine journeys.

I was subsequently hindered by public duties, since, upon the death of Johann Scheuchzer from a stomach fever on the eighth of March 1738, the unanimous vote of the governors of the Gymnasium chose me as his successor to the chair of physic and the canonical dignity. Haller, however, being called to teach anatomy and botany at Göttingen, found a suitable opportunity to complete the work. Those parts which were mine he indicated, and I had to restrain him from giving me more credit than was due to me, such was the generosity of his nature[11].

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[5] Antoine de Jussieu, 1686–1758.
Bernard de Jussieu, 1699–1776.

[6] Antoine Tristan Danty d'Isnard, ob. 1743.

[7] Johann Bernouilli I. 1667–1748.

[8] Albrecht von Haller, 1708–1777.

[9] Haller's account of this journey has been printed: *Recit du premier voyage dans les Alpes* (1728). Hausmann, A. G. St. Gallen, 1948.

[10] Johann Scheuchzer, 1684–1738.

[11] In his *Enumeratio Methodica Stirpium Helvetiae*, Gottingae, 1742, Praefatio, p. 10, Haller referred to Gesner as follows:

'Johannes Gesnerus Tigurinus ex magni Conradi stirpe natus, mirabili studio in prima juventute in plantas, & in alias historiae naturalis partes, quasi avita incitatus gloria exarsit. Vix septemdecim annos natus [1726] per *Albulam* Rhaeticam *Clavennam* iter molitus, per *Spelugam* M. & *Elmenses* alpes *Rhaetis* & *Glaronensibus* communes rediit in patriam, onustus pulcherrimis plantis, rarissimo v.g. *Ranunculi* genere, praeterviso nuperis *Rapunculi Bellidis folio* &c. Idem vicinos urbi suae agros, lacum *Felinum* et *Uetliacos* colles late populatus, ita dives plantis Belgas adiit, ut pene puer a Boerhaavio

[*For continuation of footnote see next page.*

At the time of which I speak, your incomparable writings reached Switzerland. I saw what a desired reformation they brought about in botany and natural history, and how much the study would gain in brilliancy, completeness and finish, if it were imparted in accordance with your precepts. Accordingly I desired that the History of Plants should be laid out along the lines which you laid down. I essayed to do this first with plants which were well known to me from living specimens, and subsequently with the dried specimens (above six thousand in number) which I had preserved in my herbarium, and finally with those which have been described by the more accurate of recent botanists. In this way I gained material sufficient to encourage me to revise and enlarge our work.

After this I set to work to include the *Pinax* of C. Bauhin[12] and the *Historia* of J. Bauhin[13] in my collection of notes, taking in finally the work of Ray[14] and the plants described by Tournefort[15]. In this way I had a great majority of plants precisely defined by specific characteristics, but a not inconsiderable minority remained uncertain and ill-defined. The latter I have taken care to distinguish from the former. Nevertheless, some of these are illustrated by a diligent consultation of authors and a search for specimens both living and dried.

The greatest assistance that I have received in this part of my work comes from your most accurate and authoritative writings. Thus there has been built up a History of Plants, containing a general introduction to the recognition of species, and information about their properties, followed by a classified account of plants arranged in classes, genera, sub-genera, species and varieties, together with alternative names taken principally from the illustrious Ray and Tournefort and the other leading writers on individual plants, but also from every writer whose works have appeared since the revolution in botany which you brought about. Added to these are brief descriptions of the natural habitat of each plant, a compendious description of its medical properties, with a chemical analysis, its economic and mechanical applications, its etymology, and miscellaneous observations.

I did not consider the choice of any method except your Sexual Method: than which I can find none fuller, truer, or clearer, since it derives directly from the laws of Nature herself in describing the differences according to the parts connected with fructification with such clarity and accuracy. This method, nevertheless, since it derives its transparent simplicity from its being based on the simple and fundamental characteristics of plants, is on that very score liable to certain exceptions, since Nature always strives for perfection

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in familiaritatem receptus fuerit. Post iter Parisinum Basileam redux, ubi conjuncti audivimus Johannem Bernoullium, magno mecum itinere Helvetiae partem occidentalem peragravit, quo montes *Basileensis* episcopatus, *Salevam, Gemmium, Jugumque* superavimus. Deinde anno 1729, per *Glaronensium* alpium maximam partem, iter fecit. Sequente anno 1731, alpes *Abbatiscellanas, Gamor* &c. rarissimis stirpibus divites perlustravit. Anno 1733, *Fractum* et *Regium* M. petiit. Anno 1735, cum valetudinis curandae gratia Thermis uteretur Valesiis, montem glacialem, qui ad occidentem pago thermali adjacet, utut debilis ex morbo, conscendit tamen. Idem anno fere 1732, cum primum muscos & gramina legere cepissem (nam prioribus annis absterruerat animum & legendarum, & enodandarum harum minutiorum stirpium difficultas) plurima minimarum plantarum specimina dono mihi dedit: posterioribus vero annis & nuperrime, desideratas stirpes ad perficiendum opus meum eo liberalior concessit, quod solus mittere poterat. Ipse molitus fuerat opus, quod nunc edo, cui facile par fuisset, deinde partitis viribus idem susceperamus, donec fracta valetudo Eum ab anno 1735, fere ab omnibus botanicis laboribus ad literatum ocium depulerit.'

[12] Caspar Bauhin, 1560–1624.

[13] Johann Bauhin, 1541–1613.

[14] John Ray, 1628–1705.

[15] Joseph Pitton de Tournefort, 1656–1708.

in composition. To rid myself of the embarrassment of these exceptions is a task in which no one is better qualified to be my instructor than you, my revered Linnaeus.

To me, accustomed to the method of Boerhaave[4], and having myself constructed a method reconciling that of Boerhaave with the precepts of Vaillant[16], it seems rather hard to contemplate the separation of the Gramina, Liliacea and Boraginea. I should like to ask, then, whether the Salviae might be classed with the Didynamia which are gymnoheterosperms, since the stamens of both are bifurcate, and whether the glumous flowers might be included with the Triandria, although the Anthoxanthum has only two stamens, while the Oryza and Juncus have six, and Zea, Carex, Holcus and Cenchrus have flowers of distinct sexes. The names of these genera might retain their place in your individual classes, but might be referred by the law of exception to other classes, as I observe has been done by means of suitable signs in the *Systema Naturae* which you have drawn up. By this expedient the order of your genera would hardly be altered, and at the same time some new classes would be added to the large number of the Natural Classes already defined.

As for the illustrations, I have intended them to be such as would convey a clear idea to the student and free his mind from doubts, without excessively increasing the cost of the work; so that it might be available to those who cannot afford a large expenditure on books. The parts connected with vegetation and fructification I have represented according to the differences enunciated by you, with names added so that the differences in leaves, flowers and roots, being exhibited in each table, can be perceived on a single inspection. In this I am following the great example which you set in dealing with leaves in the *Hortus Cliffortianus*. To facilitate the distinguishing of species, the differences found in the parts of vegetation can be understood from the General Tables themselves. In addition, I have in my possession the large wood blocks used by Fuchs in illustrating his work[16a], together with some hitherto unpublished, all of which I shall add to my work as an appendix, attaching the names of class, order, genus, and species. In this way I think that beginners will be led through a full understanding of the commoner plants to an acquaintance with the rarer and less frequent varieties.

As for the differences in fructification, my intention was to exhibit them by examples taken from one or more species, according to the parts reviewed by you in the Characters of Genera, representing in each table features proper to each class or order, so that the eyes of the faithful may learn at once the similarities between species and the differences between genera. Thus I hope that the imagination, which would otherwise be without guidance, may safely be assisted.

I do not, of course, forget your wise judgment on illustrations of genera, but you seemed to me to speak of the mistake by which species were represented in the place of genera: a mistake which I shall avoid if the species from which the illustration is taken is plainly indicated. It was the use of this method which enabled the great Scheuchzer to represent such a large number of species with the aid of so few plates, as Micheli[17] also did with his sparse illustrations. In this way my engraver has given a lively delineation of the parts of fructification taken from many species, some from nature, others form dried specimens, others from various authorities. Nevertheless, there are some with which I am quite unprovided, among which I should require for the completion of my illustrations examples of your genera[18] Nos 103, 104, 125, 198, 209, 300, 304, 350, 372, 380, 382, 383, 386, 435, 457, 460, 526, 533, 601, 608, 610, 622, 625, 637, 638, 687, 688, 698, 767, 797, 811, 863, and some mentioned by you among new genera.

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[16] Sébastien Vaillant, 1669–1722.

[16a] Leonhard Fuchs, 1501–1566, author of *De Historia Stirpium Commentarii*, Basileae, 1542.

[17] Pier Antonio Micheli, 1679–1737, author of *Nova plantarum genera*. Florentiae, 1729.

From this you may see, Sir, into what an ocean I have cast myself, and how great is the necessity, in the poverty of my own strength and resources, that I should have the help of others in order to swim to land. Who therefore is there better able to help me than you? From whom may I expect more prudent counsel? How I wish that out of your great learning, wisdom, and genius, you would write to me advising what should be changed, what added, and what removed, whence I might obtain specimens of genera described by you but unknown to me: so that my work might be made most serviceable for public use. It will be sufficient for me to publish only those parts which gain your approval. At the present time both the plates and the descriptions are still in separate sheets, so that it will be easy to make any alteration in their order that may be desirable.

In order to secure for myself and my illustrator a greater supply of plants, I proposed to our Scientific Society (which has been formed here for the past two years under my presidency) that they should lay out a botanical garden at Zurich; which is at this very time being adapted and laid out with plants according to your classification of genera. The plants are collected partly from our own neighbourhood, partly from the Alps: while the liberality of Gronovius, Haller, Gmelin, Staehelin[19], Gagnebin[20], and Gasque[21], Curator of the Botanical Garden at Carlsruhe, has supplied us with seeds. If God grants me health and strength, I shall next year go to the Alps in person, in order that as many Alpine plants as possible may be transferred to our garden.

My labours in other fields of natural history and my other literary activities must pass in silence, since my letter is already of an excessive length to be written to a man who is most busily engaged in works for the public benefit. But when one has begun to ask you for guidance, what end can ever be reached? One thing alone piety forbids me to pass over: I learn from a letter of the illustrious Haller, from the 'Critical Literary Journal', (*Bibliothèque Raisonnée*) and from the 'Berlin Journal' that your celebrated Society of Stockholm has decided to confer on me the honour of adding my name to those of its illustrious and learned members. I must ask you, Sir, to inform me both of what has been done, and how I may best signify my gratitude to that celebrated society. That duty I will not endure to leave unfulfilled; namely that I should by some form of service testify to my reverence and veneration for the learned society.

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[18] The names of these genera from the 2nd Edition (1742) of *Genera Plantarum* are as follows:—

103.	Penaea
104.	Blaeria
125.	Hamamelis
198.	Itea
209.	Claytonia
300.	Pharnaceum
304.	Barreria
350.	Richardia
372.	Grislia
380.	Struthia
382.	Lachnaea
383.	Santalum
386.	Moehringia
435.	Hydrangea
457.	Penthorum
460.	Gethyllis
526.	Sauvagea
533.	Isopyrum
601.	Halleria
608.	Schwalbea
610.	Craniolaria
622.	Petrea
625.	Lippia
637.	Volkameria
638.	Loeselia
687.	Heisteria
688.	Erythrina
698.	Securidaca
767.	Staehelina
797.	Tridax
811.	Melampodium
863.	Zizania

[19] Johann Rudolf Staehelin, 1724–1801.

[20] Abraham Gagnebin, 1707–1800.

[21] Mr. Gasque, unidentified.

In this matter I acknowledge my indebtedness to you, Sir, and feel that I am obliged to you especially for whatever has been done in this connexion. This was the culmination of your kindness towards me: and for my part, there is nothing I so desire than to demonstrate in my insignificant little work the esteem in which I hold your learning, wisdom and benevolence, and to shew that you have not bestowed favours upon an ingrate.

May God long preserve your health and happiness in every way. Farewell.

Written in haste at Zurich, 30th October 1748.

III. *Gesner to Linnaeus*, 5 *Jan.* 1749. [Linn. Corr., Linn. Soc. Lond.]

To the llustrious and Honourable Carl Linnaeus, Physician-in-Chief to the Royal Household, Professor of Botany at Upsala, and Secretary of the Illustrious Royal Society of that City: Greeting from Johann Gesner.

It was at the end of December, Sir, that I received your most courteous letter through the good offices of the celebrated Gesner[1] who is Professor at Göttingen. Nothing could have been more welcome, or more in accordance with my dearest wishes; since from them I learned that you—such is your kindness—had fulfilled my prayers even before my letters reached you. It was about the beginning of November when I wrote my letter in which I aimed only at one thing, namely the securing of your benevolence towards me, or more explicitly, that you would privately by letter instruct one whom you are every day instructing by your books, and that you would deign to give both advice and assistance. At the same time I gave an account of my small services to science in this country, although none knows better than I the limitations of my own powers. I entrusted this letter to that most excellent man, and firm friends of yours, as he is of mine, Mr. Gmelin[2], asking him to include it with his own letters and thus to secure for it a speedier passage. Meanwhile your most welcome letter arrived, dated the 4th of November, full of courtesy and a singular benevolence towards me, in which I see that even my wishes have been outrun by your kindness. In addition was that great honour, than which none can come more welcome to a man desirous of literary fame, that the most illustrious Royal Society of Science of Upsala had on your recommendation deigned to add me, a man both obscure and unknown in the learned world, to its distinguished gathering of men of the greatest learning and renown. This most gratifying and honourable gift, although I do not accept it without the greatest gratitude and veneration for the illustrious Society, nevertheless causes me some anxiety as to my ability to produce anything with my slight talents which shall seem worthy of so high a distinction. All that I can be sure of possessing is a lively sense of the obligation which I owe to the illustrious members, who have conferred upon me an honour which is above all recompense. There will be no task more congenial to me, none that I shall discharge with greater care and attention than any which shall seem to be gratifying to your celebrated Society. In writing this to you, Sir, who are the Secretary of the Society, a post which you fill so honourably, I make no doubt but that it will be conveyed to the Society itself. If however it is necessary to write separately to the President of the Society, I trust that you will so advise me, and communicate to me the name and rank of that illustrious scholar.

Now I reply to the remainder of your letter. I was highly pleased to learn from it of the new and valuable works which you are preparing for the advantage of us all, since I have perused to my great profit your other works, to wit, *Flora Zeylanica, Hortus Upsaliensis, Amoenitates Academicae,* and your *Systema Naturae* in the enlarged edition. In all these there is nothing that is not of value, either through the closeness of the research, the value of the method, or the practical application. But upon my life, I have never read anything of greater value to students of natural history than your *Systema Naturae*: indeed those who strive to invent new systems seem to me not to have sufficiently perceived the force of your demonstration. Nothing more useful than your summaries of the characteristics of genera has been produced in the field of botany.

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[1] Johann Matthias Gesner, 1691–1761.

[2] Johann Georg Gmelin, 1709–1755.

You ask me for a brief account of Swiss activities in botany and natural history generally. If I must write the perfect truth, and indeed there is no need to dissemble from you, nothing or very little is being done, in fact the entire study is as it were dead and buried. You are of course aware of Scheuchzer's activities during his lifetime. The well-known Johann Jacob[3], my instructor from 1713 onwards, in a brief rest from his travels compiled into the form of a book his own and others' observations, and before his death completed a History of Swiss Plants, on a plan which he described[4] in the *Transactions of the Royal Society of London*, and in the *Commercium Literarium* of Nüremberg. Johann Scheuchzer[5] the celebrated authority on grasses, after being disappointed in his hopes of a chair in botany in Padua and of Swiss history at Zurich, abandoned his botanical studies altogether and devoted himself solely to politics, and for many years had been Secretary of the County of Baden, when he was nominated professor of physic and returned to these studies. Two years later, however, he died. During his lifetime he had gathered into his possession all his brother's writings, together with his library and herbarium, leaving only the collection of fossils to the heirs. This collection is being offered for sale at this very moment. The remainder is so jealously preserved by his widow that one is scarcely permitted to inspect, let alone to make use of the material.

My own attempts and achievements in botany and natural history you have learned from my previous letter. These are my other occupations: previously I practised medicine, which, because of the custom of personal dispensing of medicines in this country, was extremely tedious, so that, being overwhelmed with work and in uncertain health, I bade farewell to medical practice, and now appear only at medical councils. About two years ago, twenty of my friends in Zurich formed a society[6] under my presidency for the study of physics, mathematics, natural history, medicine and mechanical arts: and the number of members has since been increased by many Honorary Members who make their contributions in the form of expenditure on books and instruments and the like. This year we shall see a botanical garden in which the plants will be set out and cultivated according to your celebrated method. But since this is only done by private contributions, progress is exceedingly slow.

The number of botanists in Switzerland to-day is very small. My dear friend Stehelin[7] has now for some time been unequal to his work, being much reduced by disease. The industrious and indefatigable Dr. Gagnebin[8] of La Ferrière, is making a close study of plants and is in communication with me. The celebrated Garcin[9] of Nyon is now mainly concerned with his medical practice, and has almost abandoned this study. Risler[10], the industrious chemist of Mülhausen, a keen cultivator of plants and herbs, has gained celebrity with the Catalogue of the Botanical Garden of Carlsruhe. Cappeler[11] of Lucerne, who is famous as a crystallographer even in his extreme old age, sent to me last summer some plants which he gathered on Mt. Gemmi in the Valais. My good friend Fellweger [12], formerly an acquaintance of the great Boerhaave, still climbs the Alps in Appenzell, though less frequently than of yore, and his observations of plants are less numerous, but he has trained a man to gather botanical specimens, who now sends me live plants gathered at my expense. From the same source Dr. Ehrhard[13] of Memmingen obtains his Alpine plants.

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[3] Johann Jacob Scheuchzer, F.R.S., 1672–1733.

[4] 'Botanical Invitation to forward an History of the Plants of Switzerland', *Philosophical Transactions*, vol. 37, 1731.

[5] Johann Scheuchzer, 1684–1738, author of *Agrostographia*, Tiguri, 1719.

[6] The Physikalische Gesellschaft, founded in 1746, of which Gesner was the first president, was the forerunner of the Naturforschende Gesellschaft in Zürich.

[7] Johann Rudolf Staehelin, 1724–1801.

[8] Abraham Gagnebin, 1707–1800.

[9] Laurent Garcin, F.R.S., ob. 1752.

[10] Josua Risler, author of *Hortus Carolsruhanus*, Loeraci, 1747.

I am sparing no efforts in studying the geology and the fauna of Switzerland, and in the observation of natural phenomena. I recently dissected a headless embryo, in which the heart and lungs were likewise entirely absent. In the abdomen were found various contents which I have described and had engraved. The greater part of my time I devote to public and private instruction in medicine, science, and mathematics, since I am the only teacher of these subjects in Zurich. But why should I make myself tedious to you by relating all my trifling affairs? I shall add nothing more, except to wish that you may long flourish in body and mind to the advantage of medical science. For my part, I shall never cease to cultivate your friendship with pious and dutiful affection. Farewell.

Written at Zurich the fifth of January 1749.

IV. *Linnaeus to Gesner*, 13 *Feb.* 1750. [Uppsala Univ. Libr. G. 152*a*.]

To the most excellent Botanist,

Mr. Johann Gesner,
Professor of Zurich,
Fellow of the Royal Society of Sciences of Upsala.

About a year has elapsed since the time when I last wrote to you, most illustrious Sir. As I have received no reply I feel obliged to write this letter lest I fall from the friendship of a man whom I esteem above all other botanists.

As the King has doubled our duties in this academy, the professors have no spare time, and it is, so to speak, only furtively that I can pursue botanical studies in time taken from public lectures. Last year the King sent me to *Scania*, the southernmost province of Sweden, to study the treasures of nature there. I shall write an account of my journey for publication, but in Swedish on superior orders [1]. My pupil, *Mr. Kalm* [2], professor designate at Abo, who is living in *Canada* of the Americas, has sent me a rich harvest of seeds; he has collected all the plants growing there and will bring them back with him when he returns in the spring of 1751; we shall obtain many very interesting objects from this gentleman.

I was responsible for sending another pupil, *Mr. Hasselquist* [3], to *Palestine* to study its natural history; I have recently received a letter from Smyrna where he spends the month of April when he visits Jerusalem with the Patriarch of Jerusalem who now lives at Smyrna. There, if he lives, he will collect much and almost all. A third pupil [4], but less distinguished, who last year went by ship to *Canton* in China, will now reach *Malabar* in another ship next month. From his previous voyage he brought back many specimens of the Class of *Vermes* for the Museum of our academy. A fourth pupil, Mr. Montin[5] last summer visited the mountains of *Lappland*, by the route which I took in 1732, and brought back many alpine plants for our garden ; he has discovered a new species of *Juncus*, and *Muscus Norwegicus umbraculo ruberrimo*, a species different from *umbraculo luteo*. This constitutes a new genus, on which he will soon publish a dissertation under my supervision.

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[11] Anton Moritz Cappeler, F.R.S., 1685–1769.

[12] Fellweger, unidentified.

[13] Dr. Ehrhard, unidentified.

[1] This was to be *Skånska Resa*, Stockholm, **1751.**

[2] Pehr Kalm, 1715–1779.

[3] Frederik Hasselquist, 1722–1752.

[4] Olaf Tören, ob. 1753.

[5] Lars Montin, 1723–1785.

I have discovered the *seeds* of *mosses*, concerning which someone else[6] will also soon publish a dissertation.

Three months ago we sent to press a dissertation on the *buds of trees*[7]; I have described the buds of all our trees which are wonderfully diverse in different species. Plants peculiar to very hot regions lack buds, and are unable to become acclimatized to these cold climates. Yet another pupil[8] under my direction has written a dissertation entitled *Pan Svecicus* in which are listed according to the Flora of Sweden, those plants which are eaten by cattle, goats, sheep, and pigs, and those that are shunned by them.

Such have been my small labours which I would very gladly communicate to you if only distance did not forbid. When my Scanian journey is finished and printed, I shall, God willing, devote myself entirely to the *Species plantarum*, enumerating all the certain species known to me under the genera that I have established, in order that beginners may have collected together the species examined, together with a few synonyms such as C. Bauhin's[9] or those of other outstanding works, the *Hortus Cliffortianus*, Royen[10], Gronovius[11], the *Flora Svecia*, the *Hortus Upsaliensis*, the *Flora Zeylanica*, Guettard[12], Dalibard[13], Haller[14], etc. To this I shall add many Indian species to the genera with their respective differentia.

While I am occupied in this task, you will readily understand how necessary to me is your assistance above that of all others. In order that I may include as many species as possible under their genera, I urgently require your History of Plants ! You have undertaken a herculean task which only a Swiss could accomplish ; your people achieve what they begin in a manner which no one can imitate. I rejoice with all my soul that my method did not entirely fail to find favour with so great a botanist as yourself, but it is not very clear how to combine it with a natural system. The plants themselves have been disposed by the great Creator according to their affinities, in such a manner as if they had been written on a chart or geographical map in which the boundaries between closely adjacent regions are very difficult to distinguish. They acknowledge a dual affinity which no mortal could easily overthrow. A natural system is certainly the chief requirement but, while we hold to it, it is the most difficult of all to bring to completion, since the boundaries (of the genera) are scarcely defined, as is clear today from the natural orders, where there are very obvious examples, as in *Salvia, Rosmarinus, Lycopus*, and *Monarda* with verticils, which can be indicated by a mark, and thereby ensure natural classes (orders) to be joined. Only let the natural genera be scrupulously preserved, and the problem of the orders is of lesser importance. If this is to be a method, its laws should follow from it rigorously, or everything will collapse in ruin.

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[6] *Semina Muscorum Detecta.* Respondens Petrus Jonas Bergius, Upsaliae, 1750.

[7] *Gemmae Arborum.* Respondens Petrus Loefling, Upsaliae, 1749.

[8] N. L. Hesselgren.

[9] Caspar Bauhin, 1560–1624.

[10] Adriaan van Roÿen, 1705–1779, author of *Florae Leydensis prodromus*, Lugd. Bat. 1740.

[11] Johan Friedrik Gronovius, 1690–1760, author of *Flora Virginica*, 1739–43, and *Flora Orientalis*, 1755.

[12] Jean Etienne Guettard, 1715–1786, author of *Observations sur les plantes*, Paris, 1747.

[13] Thomas François Dalibard, 1703–1779, author of *Florae parisiensis prodromus*, Paris, 1749.

[14] Albrecht von Haller, 1708–1777, author of *Enumeratio Stirpium Helvetiae Indigenarum*, Göttingae, 1742.

I hope sincerely that your History of Plants will not reach such a vast size that only few will be able to buy it. Let me know how far you have progressed, and how soon we may expect this from you. All your good friends are awaiting it most impatiently. We lack artists, or I should willingly see that you had figures of such rare genera as you may desire ; should the opportunity arise you shall have them.

I learn in letters of Mr. Kalm from Canada that many savages live on my and Gronovius's *Zizania* that grows in the fields, whence they make bread and other dishes ; this corn is very tasty.

Dr. Hasselquist reports wondrous things to us of the shellfish *Pinna* or *Penna*, which has a sentry or guard in the form of a certain naked crab which watches lest its deadly enemy sepia should destroy it.

If I send my lists to Göttingen, will you in time receive them ? In order that I may know the answer I shall send soon, and I ask you to reply that I may know if you have received my letter. I have no more time as I must discharge my duties as Rector, and I am obliged to stop this.

The Fellows of our Society each and severally bid you fare well. Give me the news of your country.

Given at Upsala the 13th day of February 1750.

V. *Gesner to Linnaeus*, 14 *Nov.* 1763. [Linn. Corr., Linn. Soc. Lond.]

To Carl Linnaeus, famed as well for his great virtues as for his learning, Physician-Extraordinary to the King, noble Knight, Illustrious Teacher and Leader in all branches of Natural Science, Johann Gesner sends Greeting.

Having sent two letters to you to Nuremberg some years ago, which were intended to be forwarded from thence to Upsala, I found myself without reply ; whereupon I began to wonder whether either of the letters had reached you, but I preferred in this state of uncertainty to admire you in silence, and to repeat your praises among those who hear me, rejoicing the while in the fruits of your outstanding labours, rather than to repeat my idle letters.

When, however, on his opportune return to his native land, a gentleman famed alike for his learning, parts and virtues, Mr. de Valtravers[1] visited my native Zurich, after saluting me with the greatest humanity and expounding the manifold obligations by which he was bound to you, he informed me with what benevolence and indulgence you regarded me and my efforts, and at the same time raised some hope that my letters would not be entirely ungratifying to you, further graciously undertaking to procure their delivery to you. This most welcome opportunity I eagerly seized upon, and I have compiled the present letter to you, Honoured Sir, in which it has been my object to speak briefly of the state of botany in Switzerland.

In the botanical studies which I have taken up, as far as my health, strength, and various obligations permit, I am indeed proceeding, but slowly, and with slower speed than others. I have taken you as the most shining and perfect example—an example which I follow at an exceedingly great distance. The plates of my work on botany (about which I wrote to you formerly at greater length) I have completed with the help of God, and have had them engraved on copper : and I now send you specimens of them, one coloured, the other in black and white, which I have entrusted to Mr. de Valtravers for the purpose of delivering them to you when a suitable occasion arises. The total number of the plates is 80, and apart from the general ones intended to illustrate the terms concerned with growth and fructification, there are several special ones which exhibit classes, orders and genera in determinate species, illustrated according to the parts connected with fructification, arranged in that lucid, uniform and fertile classification which you proposed in the Sexual Method.

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[1] Jean Rodolph Valltravers, 1723–1815, had visited Linnaeus at Upsala in 1761. (G. R. de Beer : ' Rodolph Valltravers ', *Notes and Records of the Royal Society*, **4**, 1946).

I have added the Natural Classes which you proposed in their proper places whenever the rigour of the artificial method separated them, so that the genera most closely related in nature and habit might appear in the same table. Thus in the class Triandria of the grasses, there are included with the rushes some plants from the Hexandria and Monoecia and some from the hybrid grasses, and in the place where they come in their own class, I have been content merely to indicate their presence. In this way I think that the vegetable kingdom, as though set out in an accurate map, can be journeyed over by any traveller with the greatest convenience, particularly should he be assisted by your invaluable writings. At the side of each table is added a synoptic description and account of the species, indicating at a glance both what features are common to several and what are peculiar to particular species. Numbers and letters added to the several parts represented in the table and corresponding to the text have not yet been engraved at the time that I am adding the tables to this letter. But now these are all subjected to your most learned judgment, and unless you roundly condemn them, I shall continue my efforts towards securing their publication, with a text added which will describe the species of plants, together with their uses[2].

In order to facilitate among our countrymen the most useful study of entomology, I suggested to the well-known Dr. Sulzer[3] of Winterthur that he should translate into the vernacular your incomparable System of Insects, with the addition of illustrations. He received valuable assistance in this labour from Schellenberg[4], an industrious artist, and one who has been devoted to the study of insects from his boyhood. I did indeed urge Dr. Sulzer to insert in his work all the species indicated by you, but he was unwilling to incur this labour.

Now let me explain in a few words the present state of the study of botany in Switzerland. There are few among us who are willing to undertake this study, as being one expensive in both time and money. Nevertheless there are a few who acquire some knowledge of it, either for its use in medicine or through an interest in the more conspicuous flowers. Most notable among these is my friend J. J. Ott[5], who recently published a *Sylviculture* based on Duhamel, most carefully and succinctly written, with most useful additions especially from your writings and from his own observations. The botanical garden belonging to our Scientific Society has been claimed back by the sharp practice of the previous owner, who had let it to us ; so that no exotic plants are reared among us except in the gardens of private individuals and in my own domestic garden.

We send young men into the Alpine regions to gather plants, insects, and minerals. I enclose a catalogue of plants drawn up by a student of medicine named Fueslin[6], as a result of a journey through Rhaetia in company with Dick[7], a private tutor of the illustrious Haller. In these and other matters I shall be delighted if there is anything to please or interest you. If so, you will find us ready and willing to obey all your wishes.

The work of constructing a catalogue of Swiss plants is now occupying the attention of the illustrious de Haller, my friend of many years standing. He is making use of the opportunities afforded by his position as Director of the

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[2] This work was, however, not published until after Gesner's death, when it was brought out by Christoph Salomon Schinz, under the tital *Johanni Gessneri Tabulae Phytographicae*, Turici, 1795.

[3] Johann Heinrich Sulzer, 1935–1814. Author of *Die Kennzeichen der Insecten mit einer Vorrede des J. Gessner's*, Zürich, 1761.

[4] Johann Rudolf Schellenberg, 1740–1806.

[5] Johann Jacob Ott, 1715–1769. Author of *Dendrologia Europae mediae oder Saat, Pflanzung und Gebrauch des Holzes, nach den Grundsatzen des Herrn Duhamel*, Zürich, 1763.

[6] Johann Gaspar Fuessli, 1745–1786.

[7] Johann Jakob Dick, 1742–1775. (G. R. de Beer : ' Johann Jakob Dick '. *Les Alpes*, 23, 1947).

Salt Mines near the frontiers of Valais and Savoy, practically in the midst of the Alps. Every year he sends out several botanists or seekers-out of flowers, who bring back the rare indigenous plants of Switzerland. From this arise the *Addenda*[8] inserted in various year-books and the Catalogue of rare Swiss plants published in 1761[9]. He is reserving a fuller account for the enlarged edition of the List of Swiss Plants[10]. In the labour of collecting plants he is being assisted by Dr. Gagnebin[11], physician and surgeon of La Ferrière. The doctors of Basle also make their contribution, among whom are Staehelin[12], junior professor of botany, Mieg[13], and La Chenal[14], both doctors. Risler[15] the worshipful mayor and pharmacist of Mulhausen, the author of the *Hortus Carolsruhanus*, is cultivating a remarkable garden of various flowers, aided by his son, a doctor of medicine, who has written a dissertation on *Verbascum*. In the *Acta Helvetica* may be read the various contributions of the illustrious Hofer[16] on medical and botanical subjects. There you will find *Anthericum Calyculatum* described by him under the heading *Scheuchzeria*. I have published a very few works on botanical subjects, namely a Dissertation on *Ranunculus Bellidiflorus*[17], which plant has been sent to me twice since that time, from different places ; *De Thermoscopio Botanico*[18], and *Phytographiae Sacrae*[19] in four parts. Unless these trifles are unacceptable to you, I shall take care that they are sent to you soon. Now for the sake of literature and medicine may you continue to flourish for as long as possible, and think kindly of me.

(Zurich, Switzerland, 14th November 1763).

Rare Plants collected by Messrs. Dick and Fuseli in the course of their Journey in the Alps, 1763[20].

[N.B.—rar. or r. in the following list, which is in Johann Gesner's handwriting, refers to Haller's work *Enumeratio Stirpium quae in Helvetia rariores proveniunt*, Bernae, 1760.]

I

APETALÆ Astemones.

FUNGI [Blank]

LICHENS

Lichen furfuraceus
  croceus
  Islandicus
  Nivalis
Marchantia polymorpha

MUSCI

Lycopodium an[n]otinum
  alpinum
  Helveticum
  Selago
  Selaginoides
Sphagnum palustre, *crispum*
Polytrichum com[m]une
  triquetrum

FILICES

Osmunda Spicant
  crispa
Acrostichum Septentrionale
  Marantae
Asplenium Ceterach

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[8] Haller, Albrecht von. *Ad enumerationem Stirpium Helveticarum emendationes et auctoria*, Berne, 1759, 1761, Basileae, 1762, 1764.

[9] *Enumeratio Stirpium quae in Helvetica variores proveniunt*, Lausannae, 1760.

[10] This was to be the *Historia stirpium indigenarum Helvetiae inchoata*, Bernae, 1768.

[11] Abraham Gagnebin, 1707–1800.

[12] Johann Rudolf Staehelin, 1724–1801.

[13] Achilles Mieg, b. 1731.

[14] Werner von la Chenal, 1736–1800.

[15] Josua Risler.

[16] Johann Hofer.

[17] Johann Gesner :—*De Ranunculo bellidifloro et plantis degeneribus Dissertatio*, Tiguri, 1753.

[18] Tiguri, 1755.

[19] Tiguri, 1759–63. (Seven further parts were published, 1764–73.)

[[20] See p. 239.]

II

APETALÆ Stamineæ.

Dicotyledones

CONIFERÆ

Pinus Larix
Juniperus Sabina, *baccifera*
Cupressus sempervirens

JULIFERÆ

Salix Myrsinites. Hall. r. 195
tomentosus. Hall. rar. 194
herbacea
Fagus Castanea

APETALÆ

Rhamnus Catharcticus [*sic*]
minor. Hall. r. 205
Celtis australis
Rumex Acetosella var. alpina
alpinus
Parietaria officinar. *Ocymi folio*
Polygonum Bistorta
viviparum
divaricatum
Thesium alpinum
Herniaria glabra
Scleranthus an[n]uus

III

APETALÆ Stamineæ

Monocotyledones

Gramina

Andropogon Gryllus
Bromus pinnatus [var.] quae Gr. Loliae, panicula lata Scheuchz.
Aira caespitosa var. alpina
Caryophyllea
Agrostis Spica Venti
Cynosurus versicolor
An Gr. spicatum [Alpinum] saxat[ile] crassa radice foliis junceis, spica brevissima & versicolore. Micheli ap. Tilli in H. Piz. p. 71.

GRAMINEÆ

Carex enodis
panicea
saxatilis
Scirpus caespitosus
sylvaticus
Juncus trifidus
campestris, *luteus*. Hall rar. 309
pilosus, *angustif.* var. η

IV

PETALOIDEÆ MONOCOTYLEDONES

ORCHIDEÆ

Orchis abortiva
Ophrys Monorchis
Satyrium nigrum
Serapias Hellèborine palustris

LILIACEÆ

Uvularia amplexifolia
Lilium bulbiferum
Hemerocallis Liliastrum
Bulbocodium Serotinum
Ornithogalum luteum
pyrenaicum
Asparagus Officinalis

V

PETALOIDEÆ DICOTYLEDONES

flore simplici

POLYSTEMONES

Spiræa Filipendula
Thalictrum foetidum
Aconitum Napellus
Lycoctonum
Helleborus viridis
Adonis an[n]ua
Ranunculus gramineus
alpestris
nivalis
Anemone alpina *flore albo*
flore flavo
vernalis
Clematis flam[m]ula
Atragene alpina *fl. albo caeruleo*
Potentilla recta
argentea
heptaphyllos
grandiflora
Sibbaldia procumbens
Cistus serpillifolius
salvifolius

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[20] In his *Index to the Linnaean Herbarium*, B. Daydon Jackson stated (p. 12) that the plants in the Herbarium bearing the name of Dick were ' sent by Gessner in 1763, as collected by Dick and Fuslin in the Rhaetian Alps '. This was not the case, as Mr. Spencer Savage, F.L.S., has been able to show by comparing this *list* of plants sent by Gesner to Linnaeus with those plants in his *Catalogue of the Linnaean Herbarium* to which Dick's name is attached. The two do not collate. Furthermore, many of the plants bearing Dick's labels are not Rhaetian.

PETALOIDEÆ DICOTYLEDONES (*cont.*)

DIPLOSTEMONES

Sempervivum montanum
Rhodiola rosea mas
foemina
Saxifraga Cotyledon *paucifl.*
multiflora
caesia
oppositifolia
Burseriana
caespitosa
aspera
Geranium Cicutarium
Oxalis lutea
Lychnis Flos Cuculi
Silene Armeria
Rupestris
Gypsophila alpina
Spergula arvensis
Sagina fl. majore
procumbens
Arenaria juncea
ciliata
Arbutus Uva Ursi
Vaccinium Myrtillus
Vitis Idaea
Azalea procumbens
Erica arborea
Daphne Cneorum
alpina, incana. Hall. Auctor. IV. n. 34.
Pyrola uniflora

ISOSTEMONES

Pentapetalae variae

Trapa natans
Evonymus Europaeus *latifolius*

Umbelliferae

Phellandrium Mutellina
Ligusticum Pelopen[n]esiacum
Bupleurum petraeum
Conium maculatum
Astrantia minor
Laserpitium Panax
Angelica Archangelica
Chærophyllum hirsutum

Stellatae

Asperula Taurina
Cynanchica
Galium Rubioides
purpureum

Fructiflorae

Viburnum Opulus
Lonicera Periclymenum
Campanula Cervicaria
Phyteuma Scheuchzeri. Hall. rar. 609
Plantago alpina

Rotaceae

Gentiana utriculosa
campestris
Primula Auricula *flava*
rubra
integrifolia
Aretia alpina
Androsace lactea

Solanaceæ

Phytolacca Americana

Asperifoliae

Anchusa officinalis

Dicarpae [Blank]

Difformes

Viola pin[n]ata
Allionii. Hall. r. 665
uniflora *lutea*
purpurea
tricolor *montana*

MEIOSTEMONES

Jasminum officinale
Veronica Bellidioides

TETRAPETALÆ

Myagrum sativum
saxatile
Draba alpina
incana
Biscutella Anchusae f. Hall. r. 689
Thlaspi montanum
Erysimum Cheiranthoides
Sisymbrium amphibium
aquaticum
terrestre
palustre
Cardamine Impatiens
Arabis alpina
Bunias Erucago
Cheiranthus Erysimoides

PAPILIONACEÆ

Astragalus campestris
Phaca alpina
Hedysarum Onobrychis
Coronilla Valentina
Cytisus nigricans
Spartium Scoparium
Vicia Cracca
Cicer arietinum
Polygala Chamaebuxus
ruber

PETALOIDEÆ DICOTYLEDONES (*cont.*)

DIMEIZONES
Monangiae
[Blank]
Diangiae
Antirrhinum alpinum
genistifolium
minus

Scrophularia Canina
Pedicularis rostrata
comosa

Verticillatae
Thymus Serpillum *hirsutum*

VI.

PETALOIDEÆ DICOTYLEDONES
flore Composito

staminibus liberis

DIPSACEÆ
[Blank]

SYNGENESIÆ
Capitatae
Serratula alpina
Centaurea paniculata
Carlina acaulis

Discoideae Nudae
Artemisia Absinthium
Rupestris
Tussilago alpina
Cacalia alpina
Gnaphalium luteo-album
Leontopodium

staminibus con[n]atis

Radiatae
Achillea nobilis
aromatica. Hall. r. 927
Erigeron uniflorum
Inula hirta
Senecio incanus
abrotanifolius

Planipetalae
Hieracium alpinum
Crepis hirta
Lactuca spinosa. Hall. r. 990

VI. *Linnaeus to Gesner*, 27 *July* 1764. [*Autograph lost*; *see p.* 225].

To the most illustrious gentleman,
Mr. Jo. Gesner, ornament of our time,
Carl von Linné, Knight.

Yesterday, at last, I received your most friendly and learned letter of 14 November of last year, for which I have waited impatiently so long. I do not know what leanings have led me to cultivate your correspondence above that of others, unless it be that I see in you a man honest, learned and wise in all fields: I only wish that a shorter route for our letters might be found.

Nothing gives me greater pleasure than to be able to correspond with men of solid worth, I who am unable to discuss botany or natural history in my own country, unless foreigners come who stay here for one year and depart as soon as they begin to know anything; hence I am here a barbarian and understood by nobody, and these stupid Goths mock at Latin.

When I saw your plates engraved on copper as beautiful as they are fine, suitable and select, I was thunderstruck and felt myself to be filled with new problems; nor do I know how to accept this exquisite work of yours: I embrace you in my arms, I kiss you; if any trifles lie in my power, by Flora and her flowers, I entreat you to let me know and without ceremony. Let me know what you have observed concerning the fructification of horsetails, and how the sexes are differentiated in them. . .

LECTURES AND DEMONSTRATIONS ON THE DEVELOPMENT OF TAXONOMY

In conjunction with the Systematics Association, the following Lectures and Demonstrations were given to advanced University Students during the Session 1948–49. The Lectures were given in the Society's Meeting Room, with the exception of two of the Demonstrations as stated below.

'Botanical Taxonomy up to and including Linnaeus', by Dr. T. A. Sprague, F.L.S.

'Zoological Taxonomy up to and including Linnaeus', by Dr. A. Tindell Hopwood, Sec.L.S.

'Botanical Taxonomy from Linnaeus to Darwin', by Mr. A. J. Wilmott, F.L.S.

'Zoological Taxonomy from Linnaeus to Darwin', by Dr. A. Tindell Hopwood, Sec.L.S.

'Post-Darwinian development of Taxonomy (Botany)' by Mr. H. K. Airy Shaw, F.L.S.

'Post-Darwinian development of Taxonomy (Zoology)', by Dr. John Smart, F.L.S.

Demonstration.—Taxonomy up to and including Linnaeus.

Demonstration.—Zoological Taxonomy after 1758. (*Held at the British Museum* (*Nat. Hist.*), *Cromwell Road S.W.7, by kind permission of the Trustees.*)

Demonstration.—Botanical Taxonomy after Linnaeus. (*Held at the Herbarium Royal Botanic Gardens, Kew, by kind permission of the Director.*)

OBITUARIES

Dr. **Edward Phelps Allis,** junr., a distinguished morphologist, died on 9 March 1947 at his home, the Palais de Carnolès, Menton. Over a period of nearly half a century Allis published some seventy-five papers, mostly relating to the cranial anatomy of fishes. Perhaps his most important contributions were the detailed and beautifully illustrated monographs on the head structure in various fishes, including several archaic forms such as *Chlamydoselachus*, *Amia* and *Polypterus*. He also produced a number of more theoretical articles on such subjects as the nature of the trabeculae cranii, the prechordal part of the vertebrate head, and the homologies of the myodome and trigemino-facialis chamber.

Mr. William Phelps Allis has kindly provided me with the following details of his father's life. Dr. Allis was born at Milwaukee, Wisconsin, in 1851, the second of twelve children. He studied mechanical engineering at the Massachusetts Institute of Technology in Boston, and, after graduation, he returned to his father's manufacturing business. This firm made grinding machinery for the corn and wheat of the Middle West and later became the Allis–Chalmers Company. After experimenting with an optical bench in his spare time he was led to investigate the lateral line system of fishes as a result of his acquaintance with the biologist Whitman. The laboratory assembled by Allis formed the beginning of the Lake Laboratory in Milwaukee.

In the late '80s Allis gave up his connection with the family business and after travelling in Europe for several years he settled in the French Riviera. Here he purchased the Palais de Carnolès, a former palace of the princes of Monaco, and brought over his laboratory from America. The laboratory was staffed by an assistant who made the dissections and microscopical preparations, by a Japanese artist, and by a secretary. After 1925, Allis' sight began to fail and he soon had to work entirely through dictation, the necessary papers being read to him. He continued to work, however, until 1940 when the Italians occupied Menton and he was obliged to live in a hotel in Monaco. The Prince of Monaco kindly refrained from revealing his presence to the occupying authorities and he was not molested. The laboratory survived until after the Italian surrender. When the Germans took over, trucks were sent to remove the library which has not been recovered.

The greater part of Allis' scientific work was done at his home in the south of France ; mainly for this reason he was something of a legendary figure to the younger generation of morphologists, few of whom were personally acquainted with him. His scientific contributions, however, have received general recognition and will long be studied by those who remain interested in problems of vertebrate morphology. His generosity, also, both to individuals and to scientific institutions with which he was associated, will not be forgotten.

A. d'A. Bellairs.

The Rev. **Henry Purefoy FitzGerald** (1867–1948) was the son of Lieut.-Col. R. Purefoy FitzGerald. At the age of sixteen a severe attack of rheumatic fever made him a complete invalid for five years, during which time he became very interested in botany and other branches of natural science. At the age of twenty he published a *Dictionary of English Plant Names*. Upon his recovery in health he went to Keble College, Oxford, where he took a first in Natural Science (Chemistry). He took his M.A. degree in 1896. In 1893 he became Senior Science Master at Wellington College, and remained there till 1908, when on being advised by his doctor to live an open-air life he purchased a holding in Kent and ran it successfully for eleven years as a market garden. During the 1914–18 War he turned his house in Kent into a war hospital, working as commandant, with his wife as matron. After a visit, lasting about two and half years, to a daughter on Vancouver Island, he and Mrs. Purefoy FitzGerald settled at Chandler's Ford, Hampshire, where they remained about ten years. An addition to his many-sided activities came in 1931 when he was made a Justice of the Peace.

FitzGerald was also the author of a *Handbook of Climbers and Wall Shrubs* and *Wild Flowers* (Cassell's Nature Book Series) ; he also collaborated in the *Nature Lover's Handbook.* He is survived by a son and two daughters. He was elected a Fellow of the Linnean Society on 5 December 1895. He belonged to the Conchological Society of Great Britain and Ireland of which he was continuously a member from his election on 6 November 1884.

James Hornell, (1865–1949). James Hornell was born in Manchester where his father was in business ; but the Hornells belonged to Kirkcudbright ; and his mother came from Ormskirk which lies between Liverpool and Preston. While he was yet an infant, his father's health broke down, and the family retired to Kirkcudbright where his mother remained after his father's early death. So it came about that he was educated at the Kirkcudbright Academy. Somewhere in the early eighties his mother moved to Liverpool that he might begin to face the business of life. Medicine had been thought of, but he entered a cotton-broker's office, only to find that the work which fell to him was exceedingly distasteful. He called the years over which he did it his wilderness—' a wilderness ' he wrote in the preface to his book entitled *Water Transport,* ' out of which Sir William Herdman by his kindness and interest guided ' him ' into the congenial realm of economic Zoology.'

Herdman did not create the zoologist : that began on the beaches of the Isle of Man whither he would go for holidays. But Herdman in time discovered Hornell.

From 1881 Herdman, having become the Professor of Natural History at the University College, Liverpool, had taken every chance of getting together a team of field naturalists ; and Hornell, though he could not have been enlisted at the beginning, certainly had been enlisted when in 1886 he was elected a ' Student member ' of Herdman's newest bond, the Liverpool Biological Society. Herdman had brought into being a year earlier the Liverpool Marine Biological Committee that it might promote some of his larger objectives ; through it, in 1887, the Liverpool Dock Board's old observatory and signalling station on Puffin Island, Anglesey, was converted into a biological station, and through it this was replaced in 1892 by a new station at Port Erin, Isle of Man. Also, the Committee administered funds for publishing the results of work done at these stations, being mainly a survey of the Marine Fauna. Hornell entered into the survey, worked at both stations and doubtless went on several of the periodic dredging expeditions that were made in a Liverpool Salvage steamer or any other boat that was available. He remained a Student member of the Biological Society until 1890.

One year earlier his first scientific paper was published ; it was entomological. A year later it was followed by a much longer paper on the polychaete worms of Liverpool Bay and the adjoining Seas—a paper which Herdman took into the Biological Committee's *Reports on the Fauna of Liverpool Bay.*

A trip to the Channel Islands in 1891 altered the course of his life. In Jersey congenial pursuits drew him into the company of the Sinels ; the father was honorary Keeper of the Jersey Museum and in business as a supplier of scientific material to teaching institutions, etc. ; his daughter had become a naturalist by constant companionship with her father. Hornell married Miss Sinel, and then, remaining in Jersey, entered into a partnership with his father-in-law in a double venture, on the one side to lay out a new oyster bed and on the other to open a small research laboratory fitted in the manner of those in which he had worked on Puffin Island and at Port Erin. Hornell worked with tremendous energy to make the Station self-supporting. As a means of attracting workers to its tables he started a small quarterly, *The Journal of Marine Zoology and Microscopy*, printing seventy-five copies : and with the copies he distributed zoological material which the *Journal* illustrated. He wrote almost the whole of it himself in the form of descriptive accounts of littoral animals observable on the shores of the Channel Islands. He put on sale microscope preparations of Algæ, together with micro-photographs, and he prepared lantern slides. It must have been a cruel disappointment when the venture after trial to 1897 proved unremunerative and had to be abandoned.

During these years in Jersey he contributed a few articles to *Natural Science*, one to the Guernsey Natural History Society ; and he wrote conjointly with his father-in-law a zoological chapter for a new edition of Latham and Anstey's very excellent guide book to the Channel Islands. In his *Journal of Marine Zoology* was a paper on ' The possibilities of Fishery Improvement in Jersey '.

The failure of his undertaking so threw him out of his course that he published nothing for a few years except that he salvaged what he thought worth reprinting from the *Journal* in a small book entitled *Studies in Marine Zoology* (1901). By the way of frontispiece he gave a picture of the interior of the laboratory. Earlier events must now be recalled. Pearls are known to have been fished off Ceylon and traded away as early at least as 600 B.C., and in modern times the Colony of Ceylon had come to look to its Pearl Fisheries for not a little revenue, but was plagued by its uncertaintly, as years would come frequently and unpredictably when there were no oysters to fish. Huxley, consulted in 1864, had advised that a zoologist be sent out to Ceylon to study the details of the life of the mollusc over a period of years. His advice was accepted ; but twice the investigation was started and foiled from uncontrollable causes. The third attempt, that of 1902, brought Hornell back to zoological research. At 1900 there had been no fishery for ten years; in 1901 Herdman was commissioned to proceed to Ceylon, taking an assistant with him ; and his choice fell on Hornell—Hornell who had trawled and fished with him in the Irish Sea, who had cultivated the edible oyster in Jersey and had conducted for some years a marine zoological laboratory and who, moreover, was available. Together they sailed for Ceylon in January 1902 ; together they made all the local preparations necessary, and in spring Herdman returned to his professorial duties in Liverpool, leaving Hornell to carry on with the use of a floating laboratory in the form of a native barque and a small shore laboratory set up at Galle because no site nearer the Pearl Banks had been found. What they did and how the investigation proceeded is fully set out in Herdman's ' Report to the Government of Ceylon on the Pearl Oyster Fisheries of the Gulf of Manaar ' (vol. 1, 1903). In that report Herdman wrote that he had almost weekly information from Hornell, and of Hornell that he had found in him ' such a capable and willing assistant and such a helpful and pleasant companion '. Herdman, receiving material from Hornell, distributed it to experts whose reports he edited, and the Royal Society printed them in the five volumes that go under the caption above.

At the beginning of 1904 the Government of Ceylon gave Hornell the title of ' Marine Biologist ', adding shortly afterwards that of ' Inspector of the Pearl Banks '. Under these two titles he reported to his Government on the Fishery in 1904 and to the scarcely less interested Government of Madras in 1905. He acquired the art of diving in the course of his work. With quiet enthusiasm he saw immense interest ahead and, hoping that the little laboratory at Galle would become permanent, sought to provide a library. But when it became obvious that the Government had both its eyes on revenue and neither on scientific work, he, protesting, prepared to leave as soon as the coming fishing season ended. To his good fortune the Government of Madras was at the very time arriving at a decision to organize a Fisheries Department of its own which was to collect the Fishery revenues, both marine and from inland waters, to increase the supply of fish on the markets through the take of the fishermen by introducing better methods of fishing, and having advantaged the fishermen in pocket to advance them in habits and self-respect ; also it was to control anti-mosquito operations, to educate the public in food choice, and to instruct by publications and through an aquarium. A distinguished Civil Servant—the humanistic ambitions demanded that he should know the country—was put at the head and to Hornell was offered the obviously congenial research section with the title of 'Marine Assistant', shortly afterwards altered to 'Marine Biologist'. Hornell then had to face such problems as—if fishing were done further from shore and therefore from larger boats, would it pay, seeing that larger boats would need larger accommodation in port, and the cost of providing it would be very heavy ? ; or—would the market accept unusual fish from further out ? He had also to study the primitive gear of the fishermen. This last, as the reader will appreciate, led him into Ethnology. The work sent him into many waters ; it sent him, for instance, to all the coasts of India, out to the Laccadives and still further to the Maldives, and in addition, in 1907, to Japan, China and Indo-China ; in 1909 to Arcachon on the French Coast to examine oyster beds and to Comacchio on the Adriatic to enquire into sluice-trapping in tidal swamps ; and lastly, in 1918, it sent him through the Netherlands Indies as far as Geelvink Bay in north-western New Guinea.

Zoologically his service in Ceylon is of one period with his service as Marine Biologist in Madras. During the sixteen years that make the period he published two papers on the parasites of the Pearl Oyster in collaboration with Sir Arthur Shipley, and one on the causes of pearl production in collaboration with Sir William Herdman, several on parasitic worms of Indian fishes ; one on a protozoan which causes wide mortality in fish ; one on symbiosis of an alga with the mollusc *Melibe rangii* ; an account of the Window-pane Oyster, *Placuna placenta* ; a monograph on the Indian Conch, *Turbinella pyrum* ; a revision of the genus *Meretrix* ; and a considerable number of ancillary papers. At the Linnean Society's meeting of 7 May 1914, small artificially stimulated pearls, induced by him, were exhibited.

In November 1918, F. A. Nicholson (now Sir Frederick Nicholson) was retired from the Directorship of the Fisheries Department, and Hornell was appointed to it. He held it until his own age-limit was reached in 1924.

The Madras Aquarium which had been brought into being by Edgar Thurston in 1909 as an appendage of the Madras Museum (not without consultation with Hornell), was put under Hornell in 1919. It had been an immense success as a show place and had been enlarged, but only for display. Hornell, who had asked for research laboratories as an addition to it, had failed to get them, nor did he, even after it came under his charge. The Government was averse to such expenditure ; and in 1921, after experiencing difficulties in keeping a successor to do Hornell's former work, did away with the post of Marine Biologist.

The establishment of the Aquarium had had this somewhat amusing episode :—Said the fisherfolk : 'The Government proposes to breed fish and we shall lose our livelihood'. Replied the Government wisely : 'If we exhibit the showy fish (and there are plenty of them in tropical seas) that you catch and throw back, and we do not exhibit the useful ones that you sell, will you supply to us the showy ones ?' And they did. In this way the Aquarium had become an informal zoological class-room. Hornell wrote an excellent guide-book to it in 1919, which, revised and enlarged as occasion demanded, went through a number of editions. Incidentally, he showed why various economic species of fish could not have a place in the Aquarium, because the fish do not stand the handling necessary for introduction nor can be kept alive.

As Director of his Department, Hornell's official writings assumed more the aspect of reviews. They include a very full account of 'The Fishing Methods of the Madras Presidency' (with a second part which was completed after his retirement); an account of 'The Flying-fish Fishery of the Coromandel Coast and the spawning habits of *Cypsilurus*' (1923); and 'A statistical analysis of the fishing industry of Tuticorin'. To get an idea of his many departmental activities it is well to read his Administrative Report for 1923—the last. In it he showed himself very optimistic, but the Government's reception of it was distinctly critical. I mention this as indicative of administrative difficulties which came largely from financial stringency as an aftermath of the First World War.

During his Directorship his ethnographic writings began to appear. They commenced with 'The affinities of East African Canoes' (*Man*, 1919), 'The common origin of the outrigger canoes of Madagascar and East Africa' (*Man*, 1920); 'The outrigger canoes of Indonesia' (*Madras Fisheries Bulletin*, 1920); and 'The origins and significance of Indian Boat designs' (*Mem. As. Soc. Bengal*, 1920).

No sooner had he retired than he joined the 'St. George Expedition' to the Pacific. There was a little delay in sailing from England, and, not to lose a chance, he went ahead to Madeira to look at the fishing there. He joined the 'St. George' when it arrived and it took him through the Panama Canal to the islands along the South American coast. At Gorgona he found an interest in archaeological remains, carefully investigated them and reported on them in the *Journal of the Royal Anthropological Institute* (**16**, pp. 401–32) and elsewhere. He left the boat at Tahiti, when it turned for home, to follow his quest for canoes in various parts of the Pacific, including Easter Island. This journey, together with what he had ascertained earlier, enabled him to write conjointly with Professor Alfred C. Haddon their invaluable 'The canoes of Polynesia, Fiji and Micronesia', which was published in 1936 by the Bernice P. Bishop Museum, Honolulu.

After his return the Home Government had need of him and sent him successively to Sierra Leone, Mauritius, the Seychelle Islands, Malta, Palestine and Fiji to report on the Fisheries. He was caught in Fiji by the outbreak of the Second World War and made his way home by devious routes, with this consolation, that he saw more of the World's shipping thereby. A good photographer as well as a good observer, he gathered together an unique assemblage of illustrations which, with his models, etc., has gone by bequest to the University Museum of Archaeology and Ethnology in Cambridge. In 1946 the Cambridge University Press published his *Water Transport*, a volume of about 300 pages with 46 plates, mostly from his own collection of photographs. Another book, *Fishing in many waters*, is in that Press now, and will be abundantly illustrated from the same source.

Just before his death, the Royal Anthropological Institute awarded to him its highest honour, the Huxley Medal: his death on 24 February prevented the presentation.

Hornell had read very widely in history, seeking information on transport and was very keenly aware of the necessity of proving the possibilities of transfer by human effort in all discussions of the wanderings of domestic animals and plants. This he showed in his paper to the Linnean Society (*Journal, Botany*, **53**, 1946) on the accident by which the Sweet Potato obtained a place in Polynesia when as yet America, its home, was isolated from the rest of the world. His demonstration that the outrigger canoes of East Africa are such as occur in Indonesia, with the deduction that Madagascar had very early communication with Indonesia is, like the last, an illustration of great interest, even though the earliest communication would be so stretched out as only to lead to transportation at a later time.

All the natural sciences integrate, and in these days of early specialization an investigator who, like Hornell, develops an interest in more than one science is greatly to be encouraged. I. H. BURKILL.

John Percival came of yeoman farmer stock and was born at Carperby in Wensleydale on 3 April 1863. On leaving the village school he worked for some years in Spence's Glassworks in York where his unusual qualities attracted the attention of Miss Spence (later Mrs Cotton) whose generosity enabled him in 1884 to proceed to St. John's College, Cambridge. Here he came under the stimulating influence of S. H. Vines and had what Marshall Ward later described as ' a brilliant Cambridge career ', graduating in 1887 with Honours in Part I and the following year with Honours in Part II of the Natural Science Tripos. It throws an interesting light upon his character at this time that in 1888 he was elected President of the ' Cambridge University Nonconformist Union '. Even as a boy he was an ardent field naturalist and, in his last University year, published an account of ' The Flora of Wensleydale ' which listed 653 species and varieties all but ten of which had been seen by himself. His Herbarium contains many of these boyhood ' finds '.

After leaving Cambridge, Percival spent three years in London. Mr. Carruthers, then Keeper of Botany in the British Museum, later wrote that he had ' had ample opportunity of observing Mr. Percival while carrying on his voluntary investigations in the Laboratory of the Department. His knowledge of Structural and Systematic Botany was extensive and accurate, and his investigations into unknown diseases of plants were prosecuted with diligence, ability and success. Mr. Percival brought to bear on his work a large acquaintance with other sciences than Botany, which was of first importance in prosecuting enquiries into obscure plant maladies '. During these years Percival spent much time reading omnivorously in libraries and laid the foundations of that wide and deep knowledge of scientific and more general literature that so characterized his later life.

As a student, Percival had been strongly attracted by the study of Chemistry and, in 1891, he returned to Cambridge as Junior Demonstrator in the University Chemical Laboratories. In this year the Government made Grants to the County Councils to enable them to carry out a newly inaugurated Scheme of Technical Education, and Percival joined that small, enthusiastic band of educational pioneers, led by A. D. Hall, who carried science into the rural areas. He gave numerous Courses of ' Cambridge University Local Lectures ' on ' Diseases of Plants ' and on ' Chemistry ' or ' Botany ' in relation to Agriculture to Surrey and Sussex growers, and it was this intimate contact with farmers and gardeners and the experience gained of the cross-fertilizing value of science and practice that laid down the pattern of his subsequent life.

In 1894, the South-Eastern Agricultural College was founded at Wye, in Kent ; A. D. Hall was appointed Principal and Percival became Professor of Botany, later serving also as Vice-Principal. Percival's immense physical and mental energies and his untiring enthusiasm were now canalized in the development of what was practically virgin territory. Two years earlier he had written ' The Botanist has gone on and on into minute and endless paths, far ahead of ordinary life, and is lost to the cultivator of field or garden. The gardener, on the other hand, is primarily concerned with the practice of his art, and has, by force of circumstances, specialized in his own peculiar manner, and become almost a mere machine '. Percival's aim was to wed science to practice. His first task was to acquire classroom, laboratory and library facilities for teaching and research, and to lay out and stock experimental and demonstration fields and plots. But an almost greater problem lay in the fact that there was no recognized *subject* of Agricultural Botany and no available textbook : Percival had to define and organize his field of work and then to make a first-hand study of all the common crop plants to acquire the data for his teaching—he had almost literally to create a *subject* of Agricultural Botany. In 1900 he published his volume *Agricultural Botany : Theoretical and Practical* which embodied his researches and experience. It was the first English textbook of the subject, a pioneering work, and during the next 38 years it ran into eight editions and was translated into several languages: its several editions largely shaped the pattern of the subject as it developed in University and College teaching. He published original investigations into the history, varietal development, culture, and diseases of the hop plant which laid the foundations on which E. S. Salmon was later to build so well. He assembled and described a living museum of European cereals, this being his first essay in a field which was to become the dominant passion of his life. In 1902 he published his work on the physiology of calcium-oxalate formation in *Trifolium hybridum* seedlings, and also a short but important paper establishing the causal relation of *Stereum purpureum* to silver leaf disease, a problem later elaborated successfully by F. T. Brooks.

In his early days at Wye, Percival met Ethel Elizabeth Hope Johnstone (daughter of the Rev. Edward Hope Johnstone) who was a County Council Lecturer in Dairy Science in Surrey and Sussex: they were married in 1896 and had one son, Alan, who survives together with his mother.

In 1902, Percival left Wye on his appointment as Lecturer in Agricultural Botany and Director of the Agricultural Department in what was then the University College, Reading. It was symptomatic of the man and his outlook that he 'made the establishment of a College Farm a condition of his acceptance of appointment'. In 1907 he became Professor of Agriculture and Director of the Department of Agriculture and Horticulture in the College. On the foundation of the Chair of Agricultural Botany in 1909 he became the first Professor, and held this appointment until his retirement in 1932. Percival's thirty years in Reading divide fairly naturally into three approximately equal periods.

During the first decade his activities perforce ranged widely. He established a College Farm and both here and at many outside centres conducted experiments, field trials and demonstrations. Mid-way in the period he was involved in the re-building of the entire College on a new site. Throughout the decade he was immersed in teaching and administration, and was actively engaged in building up Reading as a centre of agricultural education and research and as an advisory centre for the surrounding counties. In 1907 he served as a President of the Second National Conference of the Poultry Industry. He published investigations on such diverse topics as the house sparrow, mountain pines, weeds, hops, the structure and origin of the potato tuber, malting barley, wheat improvement, permanent grassland, the soils of Dorset, manures and manuring, new sources of nitrogen, the micro-flora of Stilton cheese, and the functions of an Agricultural College. In 1910 he published his researches on 'Potato "Wart" disease: the life history and cytology of *Synchytrium endobioticum* (Schilb.) Percl.' which laid the foundations on which Curtis and Köhler were later to build. In the same year there appeared his volume *Agricultural Bacteriology: Theoretical and Practical* which embodied his teaching and research experience: like his earlier book, this also was a pioneering work and largely shaped subsequent developments in its field. But, throughout these years of dispersive activity, Percival never lost sight of his goal—the wheat plant. He gradually added to his cereal collection and, when the College Farm became available, erected bird-proof enclosures and began to grow his wheats. By 1911 he had over 700 varieties in culture, most of them 'pure lines': the previous year he had issued his first 'College wheat', Percival's Blue Cone.

The decade from 1912 contrasts markedly with the earlier ten years since now Percival devoted his research activities almost entirely to the study of wheat. His living museum expanded rapidly and soon became 'probably the most representative collection in existence', including 'all the races of wheats, numbering nearly 2000 forms derived from almost all wheat-growing regions of the world'. Almost single-handedly he looked after this vast collection, knowing each plant intimately and tending them with loving care. He issued further ‘ College wheats ’ such as Starling, Fox, Badger, Swan and Partridge, each of which possessed valuable special qualities. But Percival was more fascinated by the botanical study of the wheat plant than by the production of new commercial varieties and over long years carried out exhaustive researches into its morphology and anatomy, growth and development, variations, hybridizations, and taxonomic relationships. In 1921 his labours came to fruition in the publication of *The Wheat Plant : a Monograph*, which brought him immediate recognition as the foremost world authority in this field : Continental cereal specialists such as Vavilov, Flaksberger, Koernicke and others paid glowing tributes to the eminence of the work. The volume embodies researches of enduring quality and, of its kind, *The Wheat Plant* remains probably the finest Monograph in the world's agricultural literature. Cambridge University gave due meed of recognition by conferring upon Percival the degree of Doctor of Science. During this period, distracted by the First World War, Percival not only prosecuted his researches on wheat and attended to a large and ever-growing teaching Department, but also, in 1918, established an Agricultural Botanic Garden, the first in the country, which rapidly developed until it became not only of interest and value in itself but also a source of research material for Agricultural Botanists the world over.

During his last ten years in Reading, Percival was occupied with teaching and administration : in 1924 new laboratories were erected for his Department ; in 1926 the University College became the University of Reading. His publications included an Address to the Imperial Botanical Conference of 1924 on ‘ The methods and value of selection in the improvement of crop plants ’, a series of valuable papers on the morphology, anatomy, and cytogenetics of species and hybrids of *Aegilops* and *Triticum*, and of *Aegilops* × *Triticum* hybrids, and smaller contributions on new wheat varieties, on wheat in 3500 B.C., and on the beginnings of agriculture. He also made a monographic study of the genus *Aegilops* based on species grown in his Agricultural Botanic Garden and on *exsiccata* from many Continental herbaria, including the loaned material of the entire Leningrad collection. When his work was practically finished he received from Eig and Zhukovsky copies of their monographs on the genus : his own study was never published and his Manuscript and Plates are in the Library of his old Department at Reading.

During these three decades Percival also found time to assemble a fine herbarium of British plants and a mounted collection of their seeds, and these, together with his Agricultural Botanic Garden, his living Museum of Wheats, and his personally annotated museum set of wheat ears, remain in the possession of the Department of Agricultural Botany at Reading. Unfortunately, his splendid library of cereal literatures was largely dispersed.

In 1932 Percival retired from the Chair of Agricultural Botany in the University of Reading but could not retire from the active prosecution of botanical research for this was the passion of his life. In 1934 he published a volume on *Wheat in Great Britain*, which appeared in a second edition only four months before his death ; in 1936 an account of his investigations on *Aegilotrichum ovata-turgidum* ; and from time to time smaller papers on such topics as the duckweeds, the cereals of ancient Egypt and Mesopotamia, and the taxonomic history of *Tropaeolum*. To within almost a few weeks of his death he was engaged in the study of seed germination and seedling growth.

Percival was a member of various Scientific Societies but his life was too full to permit him to attend many of their meetings : he was elected a Fellow of the Linnean Society in 1893, served on the Council from 1925–29, and was a Vice-President in 1926–27.

John Percival was no ordinary man. As a man of science, in a generation of great Botanists, he was of world stature and recognized as the leading Agricultural Botanist of his day. No one who met him needs reminding of his vehement and tireless energy, his ardour in investigation, his wonderful acuteness of observation, and his scholarly yet practical and resourceful mind. His many students remember him as a gifted teacher, lucid in exposition and with an encyclopaedic knowledge of Agriculture and Botany on which he could draw at will. But in Percival was something more than academic attainments. He was astonishingly versatile—a most knowledgable lover of books, an accomplished linguist, no mean artist and musician, a first-class photographer and an expert fly-fisher. Underlying all, there was in him a rare quality of spirit, simple, almost boyish, in kind but unusual in intensity and powerful to evoke response from those who in any degree had sympathies like his own. He was at one with scientist, student, and farmer but as Dr. W. M. Childs, his Vice-Chancellor at Reading and friend of thirty years, said of him ' Here was a man who with all his quick energy and exuberance kept a certain aloofness from the common world. He might possibly have been a more successful man, in the common sense, if that aloofness had been less '. It was that aloofness that tended to make him impatient of what he regarded as trivialities ; nor did he suffer fools gladly. Percival was at his best in the open country ; he was a splendid field naturalist and loved wild things and wild and lonely places, and often said ' I cannot be happy unless once a year I set my foot upon a crag '. His passion for the wilderness took him in his youth on adventurous and lonely journeys to remote Scandinavia to dwell among the Lapps, and in later years compelled him to the Alps and the Pyrenees, to the Welsh mountains, and ever and again to his own beloved Yorkshire Dales.

John Percival died at his son's home at Mortimer near Reading on 26 January 1949. His death has removed a landmark from Agricultural Science, and Agricultural Botany has lost its founder and chief architect.

WILLIAM B. BRIERLEY.

Henry Arthur Potter was born in Peckham on 16 July 1874 and died on 3 February 1949. Educated at Dulwich, he was apprenticed to the General Apothecaries Company, and later became assistant to William Martindale. Trained at the School of Pharmacy, he was admitted Chemist and Druggist in 1894 and in 1895 qualified as Pharmaceutical Chemist, being then the youngest pharmaceutical chemist in England.

In 1897 he married Amy Caroline, eldest daughter of Alfred Bonnett, of New Cross, London, who died in 1942. He later married the widow of Frederick Garon, of Southend-on-Sea and is survived by his widow. There were no children.

He was a great traveller and in visiting South Africa he made an extensive study of *Vinca Rosea*, *Plantago Psyllium* and Cape Aloes.

He was elected a Fellow of The Linnean Society of London on 4 December 1930.

Iain M. C. Talman died 31 December 1948 after a long illness contracted whilst on military service in the Royal Artillery. His studies at Glasgow University were interrupted when war broke out and it was only when he was discharged unfit, that he took his degree of M.A. He studied music in Edinburgh prior to the war and continued musical composition all through the years of his illness. Latterly, he developed an absorbing interest in natural history : paying special attention to water mites. He kept aquaria and had planned breeding experiments to discover the hosts chosen by these microscopic creatures in the early stages of their development.

Both science and art have lost a brilliant worker through his untimely death.

He married Dr. J. Murray in 1942 and their daughter Helen was born in 1947 ; there is also a daughter, Elizabeth, by a previous marriage. His father is Rector of The High School, Glasgow.

ELSIE HARVEY

Miss **Eleanor Vachell** (1879–1948) was born at Cardiff in 1879, the eldest child of Charles Tanfield Vachell, M.D., and his wife Winifred (daughter of the Rev. J. W. Evans, rector of Cossey, near Norwich). After attending a small school at Cardiff she went to The Manse, Malvern, and later to St. John's, Brighton. She was introduced to field botany by her father and from her school days accompanied him on botanical trips to Scotland, Ireland and the Continent. Later she was encouraged by the late Principal A. H. Trow. She began keeping a botanical diary at the age of twelve and continued recording her finds therein until the end of her life. She set herself the task of seeing in situ every species recognized as British, collecting it if allowable and recording it by colouring the illustration in Fitch's or (later) in Butcher and Strudwick's *Illustrations*. In the pursuit of this aim she travelled extensively throughout the British Isles and obtained a knowledge of British plants in their native habitats which could have been rivalled by but few of her contemporaries, only thirteen species at the end remaining uncoloured in her copies of the works mentioned.

Apart from the search for the rarities of the British flora the plants of Glamorgan were Miss Vachell's particular care. She was, from 1903 and jointly at first with her father, Hon. Secretary of the Committee responsible for the preparation of the *Flora of Glamorgan*, the first volume of which was later published under the editorship of A. H. Trow, and she acted as Recorder thereof for the remainder of her life. She summarized her intimate and peculiar knowledge of this subject in articles published in 1933 (A List of Glamorgan plants, *Rep. B. E. C.*, **10,** 686–743), and 1936 (*Glamorgan County History*, vol. **1**, Ed. W. M. Tattersall, Cardiff, pp. 123–178), and contributed supplementary notes thereon to the Transactions of the Cardiff Naturalists' Society (vols. **69,** 1936; **71**–**78**, 1941–7). She was instrumental with Dr. K. B. Blackburn in discovering the hybrid *Limosella aquatica* × *subulata* (*Journ. Bot.*, **77**, 65–71: 1939; and *Trans. C. N. S.*, **71**, 32–35, 1941) and published an article on the leek as the national emblem of Wales (*Trans. C. N. S.*, **52**, 1919). She also contributed a note on wild flowers to the *Western Mail* every week from 1921 onwards, the last such item being dictated from her death bed. In later years she was always most anxious to help and encourage young botanists and she watched their progress with the utmost interest. She was most generous in sharing her knowledge with others.

Miss Vachell was a keen churchwoman and an enthusiastic supporter of the British Red Cross Society, of which she was later a Commandant and finally a Vice-President. During the First World War she worked as a part-time V.A.D. at the 3rd Western General Hospital throughout its existence. During the Second World War she again set aside her beloved hobby in order to devote herself to war work, becoming Deputy Chairman of the Women's Land Army for the County of Glamorgan and acting as visiting Representative of the organization; she was also in charge of the library at the Ministry of Pensions Hospital, Rookwood, Llandaff. She inherited a strong interest in both the Cardiff Naturalists' Society and the National Museum of Wales, both of which had owed much to the late Dr. C. T. Vachell's advocacy and support. Miss Vachell became the first and so far the only woman to be President of the Society, and she also occupied for a woman a unique position in regard to the Museum: she was a member of its Court of Governors from 1919 and of its Council from 1925, and served on several of its committees, being twice Chairman of the Science Committee. She was elected a Fellow of the Linnean Society in 1917.

Miss Vachell died on 6 December 1948. She bequeathed to the National Museum of Wales the Herbarium which had been formed by the late Dr. C. T. Vachell and herself and which is to be known as the C. T. and E. Vachell Herbarium, together with her botanical diary and notes, and other botanical books and records, and she also gave the sum of five hundred pounds for the upkeep of the herbarium and records referred to. H. A. Hyde.

August Weberbauer, F.M.L.S., was born at Breslau in Germany on 26 November 1871. His first studies were carried out under the supervision of a teacher, a friend of his family, and his father, who were both of them botanists. He was educated at the high school at Glatz, Silesia, and afterwards studied the natural sciences, especially botany, at the Universities of Breslau, Heidelberg and Berlin.

He published his paper in 1893—'Ueber die fossilen Nymphäaceengattungen *Holopleura*, Caspary, und *Cratopleura*, Weber, und ihre Beziehungen zu der recenten Gattung *Brasenia*. (*Deutsch. Bot. Ges. Ber.*, **11**, 366–374.) He graduated in 1894 at the University of Berlin with the degree of Doctor of Philosophy. In 1895 he collaborated in the first edition of Engler and Prantl's *Natürliche Pflanzenfamilien*, by a contribution on the Rhamnaceae. In 1894 he obtained the appointment of privat-docent at Kassel.

Weberbauer went to Peru in November 1901, and made a collection of 5200 plant specimens after four years of study and travel. When he returned from Germany in 1908 he was appointed 'Director del Parque Zoológico y Botánico de Lima' by the Peruvian Government.

In 1911 he published his work 'Die Pflanzenwelt der peruanischen Anden in ihren Grundzügen dargestellt,' (*Die Vegetation der Erde*, **12**) and began to work on a phytogeographical map of the Peruvian Andes that was issued in 1923. Due to his friend Francis Macbride during the years 1925 to 1927 and 1929 he travelled in the Peruvian Andes studying the flora and collecting plants for the Field Museum of Chicago.

In 1925 he became Professor of Botany at the Universidad Nacional Mayor de San Marcos, and in 1932 'Botanico Adscrito a la Estación Experimental Agrícola de la Molina'. His 'Phytogeography of the Peruvian Andes' was issued in 1936 (Field Mus. Nat. Hist., Bot. Ser. **13**, pp. 13–81). During 1936–1940 he travelled all over Peru, and was chosen as a member of the 'Escuela de Altos Estudios de la Universidad Nacional Mayor de San Marcos' and given the medal 'Orden del Sol, en el grado de Comendador' for his work 'El Mundo Vegetal de los Andes Peruanos'.

In spite of his advanced age and delicate health he was in touch with nature until 27 November 1947; and retained his enthusiasm for teaching. He devoted fully his last years to the University of San Marcos and to the completion of the second edition of his phyto-geographical map.

He died 16 January 1948 in Lima. OLGA BACA DE GARCIA.

Leonard Richmond Wheeler, B.A., M.Sc. Ph.D.(Lond.), was born at Highgate on 23 July 1888, and was the third son of the Rev. and Mrs. A. C. Wheeler. He was educated at Malvern House School, Littlehampton; Brighton Technical College; and the University of London. After two years teaching at Letchworth, Herts, he obtained the post of Science and Maths. Master at the Grammar School, Antigua, British West Indies in 1912.

In December 1914 he joined the Colonial Service and was transferred to Queen's Royal College, Trinidad. He sent various botanical specimens to the British Museum, and also wrote 'The Flora of Antigua', published in *Journal of Botany*, Feb. 1916. In September 1915 he returned to England with the 1st Battalion British West Indian Regt., and later went to the Middle East with the Regiment. In 1917 he transferred to the R.F.C., and qualified as a pilot, and served in the Balkans until August 1919. After home leave, he returned as Science Master to Trinidad. In November 1921 he was transferred to the Education Department, Malaya, where he held various posts as Assistant Master, Head Master and Inspector of Schools F.M.S., and on his retirement in 1938 was Inspector of Schools, Penang. He took a keen interest in scouting, was Assistant Commissioner of Malaya, and was decorated with the Silver Wolf Medal by Edward, Prince of Wales. In 1926 he published *Scouting in the Tropics.*

While in Malaya he collected butterflies, and made an intensive study of them, and has left a valuable collection of several hundred. He has given many duplicates to the British Museum, together with some Dragonflies which include a new genus (*Depanostica fontinalis* Lieftinck, race *Wheeleri*) and two new species (*Mortonagrion arthuri*) caught by his young son Arthur at the age of three and a half, and (*Gomphidictinus wheeleri*). In 1928 he published '*The Modern Malay*'.

In 1930 he married Miss Doris Milligan, third daughter of Dr. and Mrs. R. A. Milligan of Northampton, and two sons were born in Malaya in 1931 and 1932. On his retirement he settled in Seaford, Sussex, and devoted himself to writing and his many other hobbies. He was an evangelical Churchman and a member of the Church Assembly, also Vice-Chairman of the Finance Committee, East Sussex. He took a keen interest in the Preservation of the South Downs and was Vice-Chairman of the Sussex Downsmen Society. In World War II he joined the Home Guard, held a Commission in the A.T.C., and also lectured to the Forces on the British Empire and Malaya.

His degrees were all taken externally at the University of London, and his book *Vitalism*, published 1939, was the thesis for his Ph.D.

His work *Harmony of Nature* (E. Arnold), was published in March 1948, only six months before his death on 25 September 1948. It deals with his theory of co-operation for Existence as against the Darwinian theory of struggle. His latest work *Escology of Butterflies* is still in typescript, and awaiting a publisher.

Dr. Wheeler was elected a Fellow of the Linnean Society on 2 March 1939.

Doris H. Wheeler.

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1948-49

Note.—Names of donors are given in square brackets. Separate copies of papers which are included in periodicals received by the Library are no longer catalogued.

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